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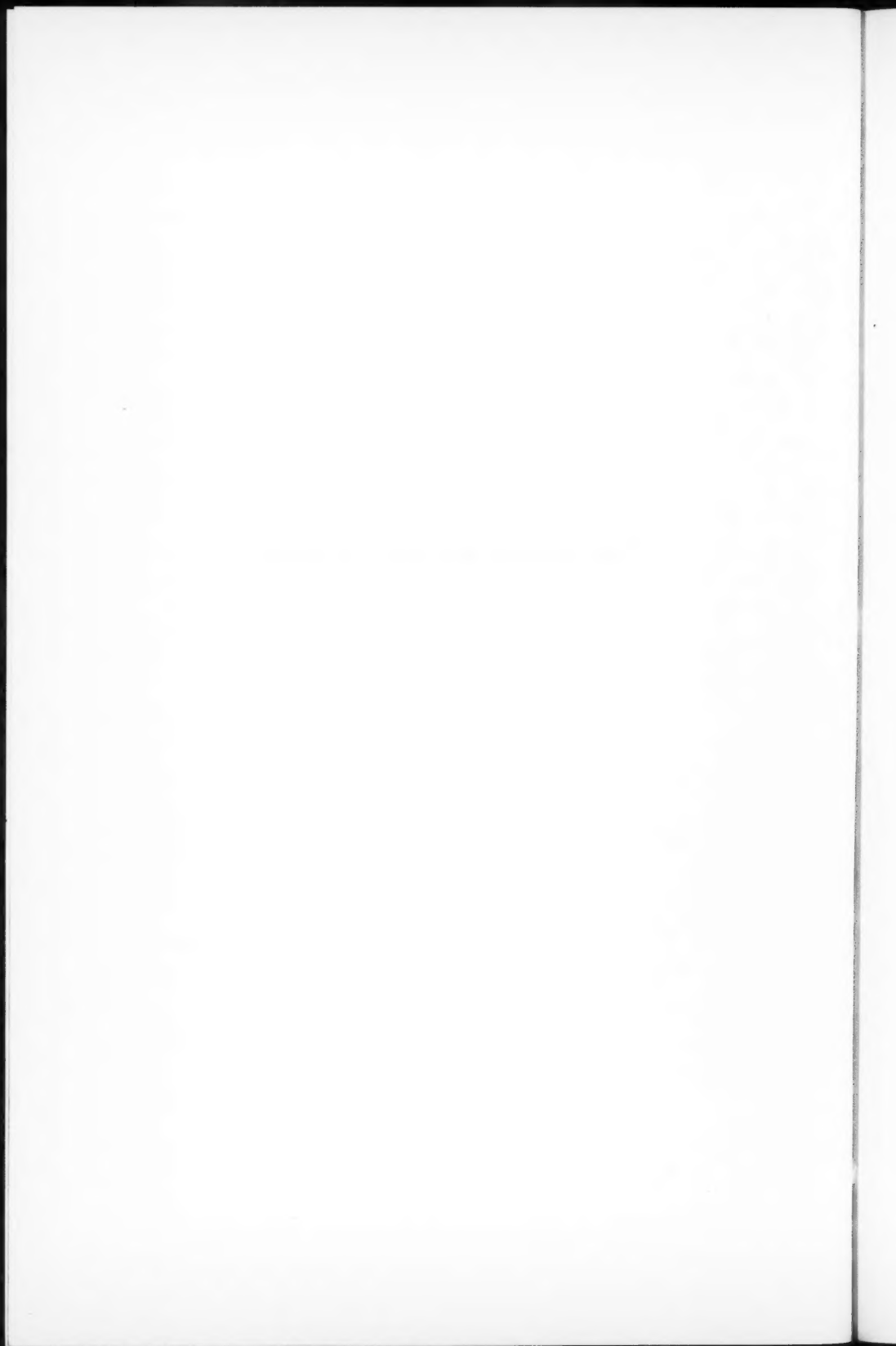
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## CORRELATED RESPONSES TO POLYGENIC SELECTION IN ANIMALS AND PLANTS<sup>1</sup>

GORDON HASKELL

John Innes Horticultural Institution, Hertford, England

Hence if man goes on selecting, and thus augmenting any peculiarity, he will almost certainly modify unintentionally other parts of the structure, owing to the mysterious laws of correlation.

Darwin: "The Origin of Species."

### THE THEORY OF CORRELATED HEREDITY

The theory of correlated responses to selection for polygenic characters was postulated by Mather (1940-48), Wigan and Mather (1942) and Mather and Harrison (1949) from studies of bristle selections in *Drosophila melanogaster*. According to these authors, both amount of free genetical variability already present and potential variability later released control the rate of change of an inherited character. Genic organization on the chromosome and also the breeding system control such variation. The extent of free variation in progeny depends on parental heterozygosity, and on the more or less balanced polygenic linkage combinations. A little crossing-over maintains hidden variation without selective change, while badly balanced chromosomes, or frequent crossing-over, reduce the amount of stored variation.

The breeding system also controls variability and the amount of maintainable heterozygosity, for without heterozygosity, as in inbreds, there is no stored variability and environmental fluctuations are quickly effectual. Much variation can be masked by phenotypic stability, even though polygenes are redistributed. Hence breaking down intra-chromosomal combinations is important in improvements involving polygenes, and heterozygosity must be maintained during selection. Non-heritable fluctuations mask new variations that accumulate.

Selection for one polygenic character usually involves changes in others due to intermingling of unlike polygenes along the chromosomes. Through natural selection polygenes have formed balanced combinations both in-

<sup>1</sup>Part of a thesis submitted to the University of London in partial fulfilment of the requirements for the Ph.D. degree.

ternally, within the chromosome, and relationally between chromosomes, with phenotypic fitness depending on this balance. Response to selection depends on unbalancing these polygenic combinations by gene recombinations following crossing-over; recombinant chromosomes can be picked out by their more extreme effects. A recombination which unbalances the polygenic combination controlling the selected character will also unbalance other combinations controlling other factors, because the polygenes are mingled on the same chromosome. Hence, in an unpredictable way, change in one quantitative character leads to changes in others; these may even upset the character undergoing selection.

These correlated responses to the selection for polygenic characters have occurred in various selection experiments on animals and plants. In some instances, such as selection for higher bristle number in *Drosophila*, the same type of selection has been undertaken by different workers. Some have recorded certain abnormalities of phenotype and reproduction which occurred during selection, while, on the other hand, other authors either have found no disturbances, or else have omitted referring to them or ignored the implications. Examples in animals and plants are given here of correlated responses and pleiotropic gene effects in correlation. These will illustrate their occurrence under diverse conditions of selection and in different groups.

#### CORRELATED RESPONSES IN ANIMAL SELECTIONS

Castle and Phillips (1914) selected in plus and minus directions the hooded pattern of piebald rats. After selection for sixteen generations this was continued to the 20th generation. In some respects this part of the series was less satisfactory than previously, as smaller numbers of animals were available from which to select, so selection was less rigorous. According to Castle (1916), the race had unmistakably fallen off in vigor or to increased prevalence of disease, or to both causes. He added, "Certain as it is, however, that notwithstanding increasing care in regard to feeding and sanitation a very large proportion of our breeding pens in the case of the selected races produce no young at all."

MacArthur (1944) studied the selection for high and low body weights in mice from an original diverse cross involving parents with different oligogenes. He found the plus selection was more effective than the minus, the increases being greater and faster than in the smaller race. He also found that in both directions the size of males changed more than that of females. MacArthur observed secondary or "satellite characters" associated with selection for body size, and the races selected solely for body size eventually differed markedly in several other respects, such as hair color, ear-length, comparative length of appendages, e.g. tail, and litter size. Growth in body size is the primary, or essential, character, and selection for this brings with it these satellite characters clustering around and correlated with it. These differences, it was pointed out, are due to expression of different basic metabolic levels. In the smaller race

there is a tendency for dominant oligogenes to be selected for, while in the larger race the recessives for qualitative characters become homozygous. It is known that in mice the genes *b* and *d* have pleiotropic effects in accelerating growth and *B* and *D* and *s* retard growth, although Dawson (1932) found little evidence of linkage between genes for wildness and tameness, and albinism, agouti and brown in mice. MacArthur maintained that, regardless of the pleiotropic action of these qualitative genes on body weight, selection for increased size would have succeeded without these effects or in spite of them.

Generally the various organs and regions of the body do not change at the same rate as the body. The various correlations are due to endocrinal links; general body size factors exert an indirect control over the litter size, rather than that the two races carry different litter-size genes or fertility factors. MacArthur stated that correlated responses would not be unexpected unless there was a single specific gene for each character. Correlations due to linkage or drift would be sporadic and erratic, while those due to manifold gene effects were more likely to be more regular and widespread. He suggested that rules could be made, e.g. many mammalian species have large body size associated with large litters. Here the several effects would not be clearly separable if genes act pleiotropically. Changes in body size would lead to changes in the relationship of body surface to mass and also in metabolic levels and activity.

MacArthur also pointed out that size genes are in some degree genetically linked in many or all the chromosomes with qualitative, multiple, balancing or modifying factors controlling other characters. Following crossing-over there is variability in several respects and quantitative and qualitative characters are released by new combinations. Characters in such a complex are held together, at least briefly and are changed concurrently by selection directed on any one of them. According to MacArthur "Modern genetic theory thus returns, after a long diversion, to the general principle emphasized by Darwin, that selection produces correlated, rather than a series of independent changes."

MacArthur suggested too that correlated changes are obviously adaptive, but this point is open to question. Is large litter really an adaptation for large size in mouse? There is no adaptation in, say, increased number of nipples for feeding the young. He considered that groups of correlated characters are frequently adaptive enough to become established in nature by natural selection, and referred to the climate rules of Bergman and Allen in relation to animal distribution. Such complexes of associated characters would often be worked over and extensively reorganized in nature. His selected races had become rather like the geographic races of mammalian species occupying opposite ends of a temperature cline in nature.

With some exceptions, larger races of domestic animals have larger litters and this is true for man. Thus MacArthur maintained that "selection becomes a powerful tool for the breeder selecting a simultaneous improvement in these useful characteristics," such as large litter and body

size, faster growth and more efficient reproduction. Finally, he recalled that differences between his mouse races are determined not by special fertility genes but, in a great part at least, by the same common and general multiple size or growth factors that control body size.

MacArthur's experiments were strongly criticized as to accuracy of method by R. R. Gates at the American Association for Advancement of Science meetings in Chicago, December, 1947, and these criticisms were later strenuously denied (cf. MacArthur, 1949). It appears that MacArthur was unaware of Mather's work on the subject. He arrived at similar conclusions, and independently recognized the implications. MacArthur's results are tabulated in table 1; they support observations made by Goodale (1937).

Some years ago Strong found that injections of methylcholanthrene in mice produced tumors in them in greater quantities than uninjected mice.

TABLE 1  
CORRELATED RESPONSES IN MACARTHUR'S MOUSE SELECTIONS.

MACARTHUR'S MOUSE SELECTIONS	
HEAVIER LARGER RACE	(By weight)
LIGHTER SMALLER RACE	
PSYCHOLOGICAL { Tamer and more docile; sluggish and obese. }	{ Very active, aggressive, rather savage; agile and elusive (difficult to catch). }
MORPHOLOGICAL { Solid, or self-brown, or Cinnamon (occasionally albino); Often dilute Body length longer. }	{ Intense black, black and tan, or agouti, frequently piebald; Never dilute or albino. Body length smaller. }
PHYSIOLOGICAL { Number of young in litter increased (3 to 15). Primarily due to super-ovulation, i.e., number of ova available. More prolonged and accelerated growth of body. }	{ Number of young in litter decreased (3 to 8).  Retarded growth rate of body. }
Relative appendage lengths differ.	

Injection of methylcholanthrene into a series of mice for many generations has produced the following phenomena (Strong, 1948):

1. Germinal mutations involving hair color, eye color and distributional patterns of pigmentation.
2. Somatic mosaics that are composites of two genotypes.
3. Germinal mutations altering susceptibility to the appearance of fibrosarcoma arising at the site of injection of carcinogen.

4. Production of germinal mutations influencing the occurrence of specific types of tumors that arise not only following injection of carcinogen but also subsequently in their untreated descendants.
5. Embryological and physiological disturbances that may not be genetic.
6. Conversion of a low incidence strain into a very high one.

Strong (1947) has also recently summarized his results on resistance to tumor formation following methylcholanthrene injections. He hybridized mouse lines and the hybrid offspring were continued for many generations by brother-sister matings, all being inoculated by an overwhelming dose of methylcholanthrene. He always bred from the most resistant pair of mice of each generation. This selection for tumor resistance gave what Strong called a "kaleidoscope shift" in the types of induced tumors which appeared in this order:

1. Local tumors at injection site.
2. Surface spread of tumors over the whole body.
3. Tumors in the thoracic cavity.
4. Tumors in the abdomen.
5. No tumors at all.

Stage 5 was of short duration and continued selection toward resistance to all tumors led to a reversal of susceptibility leading back through stages 4→3→2→1; tumors appeared earlier at the injection site than in the early generations.

According to Strong (1947) the gradually increasing resistance to tumors in succeeding generations is due to accumulation of recessive genes for "normality." The reverse trend to greater susceptibility may be due to new mutations due to the influence of methylcholanthrene on the germ plasm. Strong gives as evidence in support of this: (a) linkage and crossing-over between cancer-susceptible genes and brown hair pigment genes. (b) In stage 4 there are many changes in coat color, eye color and distributional patterns of pigmentation. (c) After adenocarcinoma of the gastric mucosa in stage 4 the same lesion is established in untreated descendants. (d) 1 percent spontaneous tumors in the original stock compared with high incidence in injected strains with subsequent untreated descendants, i.e. cancer-resistant strain, becomes a cancer-susceptible strain by chemical means. (e) Many embryological and physiological disturbances (e.g. production of giant mice, alterations of fertility and fecundity) and endocrinologic disturbances (e.g. vagina abnormalities and precocious senility).

It is quite feasible that methylcholanthrene, like the nitrogen mustards, is mutagenic as well as carcinogenic. Yet the types of abnormalities that appeared during the resistance to tumor selections bear remarkable similarity to those that appeared in MacArthur's weight selection experiments, which can justifiably be ascribed to correlated responses. Cancer resistance or susceptibility is under polygenic control; selection in either direction will bring about recombinant types and so morphological differences appear. The distributional pigment patterns that appeared also bear remark-

able similarity to the black abdominal patches observed by Mather and Harrison (1949) in the high bristle selections of *Drosophila*.

Agar, Drummond and Tiegs (1948) have repeated McDougall's classical experiments with rats which had the choice of receiving an electric shock or not after emerging from water. Their experiments were taken to the thirty-sixth generation. They found various other differences between trained and untrained lines. Rats of trained lines were bigger and heavier and there was a difference in color pattern which has maintained itself. There was no difference between size and learning rate. The results were interpreted in that three independent differences of a hereditary kind had appeared, one temporary and two permanent. Their general conclusion was that even selections based on the supposed fixity of inbred lines must be treated with caution. The experiments, however, may also indicate the principle of correlated responses.

Studies of selection in *Drosophila melanogaster* have been made by several workers, and these were especially prominent in the early days of modern genetics. MacDowell (1915) with bristle number, Zeleny (1922) with facet number, and Sturtevant (1918) with dichæte, all carried out long-term selections in high and low directions. More recently Wigan and Mather (1942), and Mather and Harrison (1949) have added to these investigations. Some of the earlier investigators had noted *en passant* that mutations and lethal factors appeared in the selection lines, regardless of whether these were in a plus or minus direction. For instance, Zeleny (1928) selected for high and low facet number in a white bar-eyed race of *Drosophila melanogaster*. Besides mutations to normal eye and ultra-bar, he found between the 21st and 28th generation a sex-linked lethal factor which increased facet number, but this was eliminated. A full-eyed mutation occurred four times in the high line and three times in the low line, while ultra-bar appeared once in the low and once in the high. Zeleny noted that "several other very low individuals that died without offspring were probably ultra-bar also." A sex-linked lethal factor appeared in the 21st generation of the high line; this caused increased facet number.

Similarly Sturtevant (1918) noted that a mutation, called "Extended," appeared in a selection line of dichæte. This could, of course, be readily interpreted as a simple mutation occurring by chance. Yet one wonders whether polygenic selection may actually increase *mutation rate* of oligogenes, i.e. the relationship of unusual combinants in the same cytoplasm causes an internal disturbance which encourages mutation in addition to the correlated response effects. To test this an analysis of oligogenic mutation rates in unselected and polygenically selected stocks could be investigated. Mather and Harrison (1949) described a number of correlated characters which appeared in their cultures during their investigations into the manifold effects of high and low selection for bristle number in *Drosophila melanogaster*. These correlations may be summarized as follows: (a) *Spermathecae*. The normal number is two; in later generations of selections all degrees of pleio-spermathecae were obtained with grades rather

like those of the distribution of pleiocotyly in plants. They found that selections of bristles in a certain direction both raised and lowered the frequency of pleio-spermathecae and affected one class of abnormalities while leaving another without significant change. Mather and Harrison have interpreted this as showing that simple pleiotropy is inadequate to account for correlated responses. They were not able to establish a maternal effect. (b) *Discriminative mating*. There was a suggestion that a mating behavior difference between two wild strains depended on more than one gene and that correlated responses occurred in this character. (c) *Sterno-pleural bristles*. The number was altered by the selections in a fairly regular fashion corresponding to abdominal bristle number. This was interpreted more to a physiological change more likely due to pleiotropic action of bristle genes, as they do not show the irregularity associated with correlated responses due to linkage, but with smaller irregularities due to a breakdown in linkage being superimposed on the regular effect of pleiotropy. (d) *Coxal bristles*. These may also be interpreted as due to pleiotropic action, although not the same as for sternopleurals. (e) *Abdominal pigmentation*. Patches of lighter body color were clearly seen on the sides of the dark areas of male flies. These were attributed to correlated responses following unusual crossing-over. (f) *Small eyes*. Only one eye of an affected fly showed this aberration; it was not due to a chance mutation nor a simple gene, nor a simple pleiotropic effect. (g) *Chromosome behavior*. Some polytene chromosomes showed a non-specific incompleteness of pairing between homologues.

There is little doubt that selection has brought with it correlated changes in other respects of the phenotype. Svårdsson (1944) also found that a selective change in fin ray number in *Lebistes* gave a decrease in fertility.

#### CORRELATED RESPONSES IN PLANT SELECTIONS

Examples of correlated responses that have occurred in experiments dealing with the selection for polygenic characters in plants have not been so frequently reported. An example of economic importance is that of Winter's selection experiments with maize (Winter, 1929). Seed from Burr's White were selected in four directions. The method, to give one example, was to select 24 ears richest in protein and to plant these in an isolated plot. Each ear-to-row was harvested separately and seed for the following crop was taken from ears with highest amounts of protein. After nine years, a modification was introduced: alternate rows were detasseled and seed selected from highest yielding detasseled rows. Later, in order to reduce inbreeding, two seed ears were taken from each of the detasseled rows regardless of yield. There was great difficulty in overcoming the effects of inbreeding although the lines were still reasonably heterozygous, as direct inbreeding still produced depressed vigor, although they became more rapidly uniform than unselected material.

Winter found that the Low Oil strain approached a "physiological limit." As most of the oil is in the germ, selection for low oil content had de-

creased germ size, not only absolutely but also relatively compared with endosperm size. Thus the ear of the lowest oil content (0.69 percent) had 80 percent germless seeds. Winter observed, "The necessity of using ears having grains that will germinate naturally tends, therefore, to check the progress of selection, and eventually may stop it altogether."

Woodworth, Leng and Jugenheimer (1952) have since carried these selections to fifty generations. They find that all selected strains have been considerably modified in several morphological and agronomic characters. These include differences in ear, kernel and germ sizes, starch textures, and ear row numbers; there are also differences in maturity, plant height, ear height, tillering tendency and susceptibility to leaf firing under deficiency of available nitrogen. Moreover, their grain yield is now only half that of adapted hybrids in Illinois.

In the John Innes sweet corn cold hardy selections (Mather and Haskell, 1948) some of the lines showed the pseudo-starchy condition but the varieties started with were still recognizable after several years' selection. The sweets were still not in any respect confused with the hardy starchy line also used. Also in maize there is a single gene difference which is responsible for the starch/sugar condition of the endosperm. Jones (1919) was able to select sweet seeds from an  $F_2$  cross of dent by sweet into two directions. Selection of most starchy appearing individuals for ten years with self-fertilization for nine generations gave the seeds an appearance of pseudo-starchy. On the other hand, the most sweet appearing individuals were selected, following self-fertilization, for nine generations; these gave only translucent, wrinkled seeds. However, examination of starch grains of normal, pseudo-starchy and sweet seeds showed size differences; in external appearance and in gross chemical analysis, in the nature of their starch grains and texture of the endosperm, pseudo-starches are more like sweets.

There is no doubt, as shown by the series of sweet corn inbreds of different maturity ratings produced by W. R. Singleton in Connecticut, that the earliest inbreds are more prone to have ears with pseudo-starchy seeds, as in C4, than later ones like C95. This also applies to the hybrids of different maturity ratings combined from these inbreds. Table 2 traces seed characteristics according to maturity rating.

TABLE 2  
CORRELATED CHARACTERS IN SEEDS OF HYBRID SWEET CORN  
OF DIFFERENT MATURITY RATING

Maturity rating	Variety	Seed type	Seed quality
Early	Spancross	often pseudo-starchy	dull
	Marcross	sometimes pseudo-starchy	not so dull
	Carmelcross	clear	somewhat dull
	(17-3 x 33)	clear	bright
	Grant	clear	bright
Late	Golden Cross Bantam	clear	bright
	Evergreen hybrids	clear	bright

Another example of what appears to be a change in a quantitative character resulting from selection of another is that of the recent discovery of a high sucrose inbred field corn C103 in Connecticut (Singleton, 1948). C103 had been carefully selected for a stout and unbreaking stem, which is valuable to withstand lodging. This was correlated with the number of vascular strands running up the stem. It had been noticed that the stalk of this inbred resembled that of sugar cane. This led to the stalk being tasted and it proved to be nearly as sweet as sugar cane. Singleton observed that "it seems that the sugar content is not a function of the same gene or genes causing the stiffer stalk as C103 stem behaved as dominant and the sugariness as recessive in crosses." Similarly selection for high and low positions of ears on the main stems in maize have led to rapid differences in five generations. Plants with low ears were much shorter than those with ears higher up the stems (Babcock and Clausen, 1918).

Selection for maximum yield in sugar beet, as measured by total weight, usually results in increased water content but not in dry matter. Similarly selection for high yield in oats brings about an increase in starch and not in minerals and proteins. A balance between various quantitative characters has therefore to be maintained by plant breeders during selection.

Using seedling cotyledon number, called pleiocotyly, as selection criterion, Haskell (1949) has produced correlated disturbances in the normal balanced condition of adult dicotyledonous plants. Pleiocotyly selection, with a gamut from monocotyly to tetracotyly, was practiced on outbreeding species in the family Cruciferae, on partly outbreeding species in the Umbelliferae and on inbreeding species of Solanaceae. Selection increased the frequency and range of pleiocotyly in both outbreeding groups but with inbreeding species, e.g. English varieties of tomato, it was ineffectual within the limits of the experiment. In various economic forms of *Brassica oleracea*, such as cabbage selected for pleiocotyly, some selections gave pleiocot seedlings which grew either into normal or abnormal adults. The types of morphological abnormalities which occurred could be classified as: fasciations, chloroses, dwarfs, multiple branchings, irregularities of shape, weak growth and alterations in anthocyanin intensity. Most of these must be considered as disturbances in hormonal balance.

Although the disturbed growth may be due to pleiotropic effects of genes controlling pleiocotyly, phenomena such as lowered fertility, increased occurrence of lethals, chloroses and reduced vigor indicate other genes are also involved in producing these correlated changes.

If Strong's cancer results are correlated responses, the "kaleidoscope shift," which may be interpreted as due to progressive crossing-over, thus suggests that in selecting plants for extra cotyledons, the maximum degree of pleiocotyly eventually will be reached. Further selection for this will then direct selection back again once the peak has been reached and former types of correlated responses will again appear. There is a limit to which selection can be taken depending on the number of genes controlling the character; once the limit is reached, selection will still produce recom-

binants in other polygenic effective factors but these now are similar to those that have previously been produced in earlier selections. However, support for this hypothesis must depend on an examination of continued selection for pleiocotly.

In the realm of plant ecology, certain types of flora are associated with a particular environment, and many diverse families take on similar adjustments to it. For instance, selection for xerophytic conditions has rendered similar morphological changes in Cactaceae, Euphorbiaceae and Crassulaceae; these succulents are adjusted to water-storage. Selection by the environment for plants more adaptive to water-holding has brought with it correlated morphological changes of a similar nature in different families. Similarly, study of island flora characteristics should produce evidence of correlated responses.

It is known that in general there is a correlation between, for instance, root spread and area of the canopy of leaves, or root depth and stem height. It may therefore be asked whether this is a mutual physiological adjustment of the parts to obtain the greatest benefit from precipitation or due to correlation in the activity of the root system as a response to selection for a particular type of stem branching system or *vice versa*. Is this a compensating physiological adjustment or an example of correlated response? Or perhaps a combination of both? One is therefore led to speculate whether correlated responses, as a result of selection for a particular type of environment, have not sometimes caused the confusion that has given rise to the support of the inheritance of acquired characters amongst some biologists.

#### CORRELATED RESPONSES IN MICRO-ORGANISMS

Now that Lederberg (1947) has produced evidence of chromosomal inheritance in bacteria, it is possible to reconsider the problem of the transformation of pneumococcal types with nucleic acids. There are 40 different types of pneumococcus and these types have never been shown to undergo spontaneous transformation from one type to another, although the reversible conversion of "smooth" into "rough" occurs in many types. By means of desoxyribo-nucleic acid it is possible to transform, or transmute, an attenuated, non-encapsulated rough (R) variant derived from one specific type into a fully encapsulated, virulent, smooth (S) cell of a *heterogeneous specific type*. Stacey (1947) in reviewing this subject states that, "There is no doubt that this is an authentic case of a specific mutation caused by a chemical entity, and its importance cannot be over emphasized." Stacey speculates on the nature of the change: (i) R cells must be in a state of competence before transformation can be achieved; (ii) the transforming mechanism must have a connection with, or is part of, the enzymes which synthesize capsular polysaccharide; (iii) the transforming mechanism forms part of the chromosome system. But it is not impossible that we have here selection acting on a polygenic character for specificity and

that this change, correlated with it, has altered the type from rough to smooth.

The amount of chromosome material and their number must be limited by size in bacteria; selection for any particular genetic characteristic, whether physiological or chemical, would therefore rapidly produce correlated responses. In view of the rapidity of reproduction in this organism the appearance of such changes soon after submitting them to a new (chemical) environment would not be unexpected. However, the present writer puts forward such a viewpoint with all caution.

One might likewise also postulate that the changes that take place in some viruses during their passage through intermediary hosts are due to correlated responses following selection of viruses more adaptive to new environmental conditions. Many examples are known (cf. Bawden, 1943) of these so-called "mutations"; there is the example of attenuation of the sugar beet curly top virus by passage through *Chenopodium murale* and the restoration of virulence towards sugar beet by subsequent passage through *Stellaria media*. This phenomenon, according to Bawden, may be explained either by a mutation in one direction and then its mutation in the reverse direction; or the virus is a mixture of two strains with differential powers of multiplying in the two intermediate host species. But it is also possible with such a rapidly dividing organism of limited volume, that selection is producing correlated chemical responses and that as the limits of selection are not reached the correlations can proceed in both directions, according to which way selection is acting.

#### CORRELATED RESPONSES IN PLANT-BREEDING

Correlations in plants have been known for a long time. Darwin (1899) described many examples of correlated variability in both animals and plants, but was naturally unaware that there were several explanations for them. These include pleiotropic effects, e.g. anthocyanin in various parts of a plant, or in animals the pleiotropic effects in development of the type described by Grüneberg (1938), and linked genes.

There are also correlations between oligogenes and polygenes which results of selection have indicated. For example, some peas have crinkled seed while others have round seed. Of the first early types, only varieties like Early Superb with round seeds can be sown in autumn, as they withstand the cold weather. Other examples in maize, tomatoes and barley have also been tabulated by Anderson (1939). Thus correlated responses following the breakdown by selection of a stable character such as dicotyledony, which is polygenically controlled, may also be expected to include morphological changes controlled by oligogenes. It is well known that Luther Burbank claimed to be able to discriminate between useful and useless types of progeny by examination of large numbers of seedlings. He maintained that there was a strong correlation between seedling and adult phenotypes. This, as my experiments with pleiocotylous seedlings have shown, is true so far as adults differing from normal can be obtained.

No rules are yet available, other than that showing a general reduction in viability and fertility is to be expected, to predict what changes the adult will show. Correlations are known in fruit trees, small foliage of seedling tending to go with small fruits and dwarfed seedlings tending to produce poor plants. Thus it is to be expected that selection acting at the seedling stage also brings about correlated changes in the adult characteristics. The studies in pleiocotyly lead one to believe that natural selection acting at the seedling stage, through competition and other causes, was a powerful factor in influencing polygenic evolutionary systems. Many lethal genes manifest themselves in the seedling stage and are eliminated; similarly many less favorable combinations of polygenes would be eliminated at this stage. Through correlated responses, changes would thus continually manifest themselves in the adult characteristics. They have been one of the many factors that have given rise to the vast array of plant types, so vividly seen not only in living types but also in the fossil record.

William Bateson in his presidential address to the British Association in 1915 queried, "whether we are limited to the old view that evolutionary progress is from the simple to the complex, and whether after all it is conceivable that the progress was the other way about." It is of interest to consider what bearing the theory of correlated responses has on this interesting speculation. In my pleiocot selection experiments it was possible to get a range of pleiocotyly from one up to four or more with all intermediary stages. Dicotyly has, apparently, resulted from phylogenetic decrease of a more elaborate state, and natural selection still has the opportunity of further reducing all dicotyledonous flowering plants to the monocotylous state. What is even more pertinent is whether the correlated phenomena associated with selection for pleiocotyly are reversions to a simpler or to a more complex state. If the effective polygenic factor for dicotyly is now in a balanced condition in dicotyledons, then it is quite feasible that effective factors of other polygenic systems are also in a state of balance. Many of these polygenes of different effective factors are linked on the same chromosomes. Selection for recombinants of one type in the direction of the more primitive condition, *viz.* polycotyly, might therefore be expected to produce correlated changes also in a primitive direction in other effective factors. We may query, therefore, whether such phenomena as multiple branching, or even fasciations, are reversions to a primitive condition. Continued selection for pleiocotyly should thus break down the present equilibrium of the species and release variation, with the production of more primitive characteristics.

Cultivated plants are the results of conscious selection of wild species by man over very long periods. Such selection has tended to reduce variation and some cultivated species are at the limits of effective selection e.g. many open-pollinated varieties of maize can no longer be selected for increased yields. In inbreeding species such as peas selection within a line, as Johannsen showed, is ineffective; only mutation can produce changes upon which selection can act. In some instances, as with beet

and carrot, it has been possible for breeders by selection from the wild to recreate strains similar to the cultivated ones already in cultivation. But this would not be easy for most species, as the chances of getting the desired mutations, crossings-over and segregations would involve many generations and much land would be required. This is where the application of correlated responses might be utilized. By selecting a character such as cotyledon number, variations of other characters can be released in an apparently stable species and these variations tested for their use in plant-breeding. After crossing the types which are of interest, back selection of the basic character (dicotyly in this instance) will tend to re-establish a condition of balance and stability. Similarly by releasing variations in two, say, cabbage varieties and crossing these followed by back selection, new hybrid strains could be obtained. These would combine characters of both parents, and possess secondary characteristics which otherwise would not have been released and therefore not present in the ordinary hybrids. At this stage it is not possible to say whether, once new morphological types have been produced, it will be possible to stabilize them. It is thought that selection of dicots from pleiocot cultures in the pleiocotyly experiments might be a means of so doing.

Hutchinson, Silow and Stephens (1947) in discussing the nature of genetic variability have already suggested, on the basis of MacArthur's mouse selections, that correlated responses may play an important role in plant breeding. They give as an example the results of Hutchinson and Manning with U4 cotton. This strain was originally variable and the breeding system they adapted was to conserve variability. But they found that although the differentiation achieved to local conditions was great, there was still sufficient variability left upon which the plant breeder could work. Continued selection in one direction continued to release variation in others, and the variability which is maintained enables the breeder to select for other properties. Yet the fertility changes that occur with continued selection offer a warning to those breeders who would aim relentlessly to select their species in one direction only. Relaxation of selection would be necessary to maintain fertility unless the character selected can be maintained vegetatively.

It has not been possible from the writer's selections to find any types, from the variability that had been released by selection for pleiocotyly, having practical value, although Litovchenko (1940) in Russia has already advocated the wider use of tricotyly.

#### CONCLUSIONS

If selection is looked at from a broader front, it will be seen that the types of selection that have been described here are all specialized. They represent a lop-sided aspect compared with selection for all-round animal and plant improvement. This may indicate, for instance, why cultivated plants have been improved in their vigor, seed production and general plant characters without presenting deleterious responses. They have been se-

lected for all-round improvements which maintain the general balance of the plant. Thus, for example, Rasmusson (1932) found that selection of mangels for root length not only affects that character but also root weight, dry matter percentage and liability to bolting. But due to the opposite effects on root weight and dry matter percentage there is no effect on dry matter yield per root. Thus only a slight change occurs in this character even when other characters are distinctly changed.

It is clear that many cultivated crops have been improved by mass selection; Vilmorin's selections with carrots are well known. Similarly mass selection was useful in producing marketable types of cotton. But such selections were maintained in keeping with the general welfare of the plants. Any specialized selection which interrupts the adjustment of a species to its environment will bring about correlated responses which could interfere with the general balance of the plant, not only internally but also with the external environment.

Thus from the evidence of correlated responses following specialized polygenic selection, the writer concludes that although this releases variation, which is of some value when the species is undergoing environmental changes, from the animal and plant breeder's view-point it can be dangerous in an already adjusted species if the specialized selection is carried too far in one direction. Selection for a character like earliness taken too far will produce plants that are either too small or too weak to produce good fruits or large amounts of grain. A balance must be made between artificial selection and the general balance of the species, which has been built up by both natural and human selection through the ages. The alternative to continued specialized selection of polygenic characters would be re-selection of the polygenes controlling major mutations in the required direction.

Mutations, both deleterious and advantageous, occur in economic crops and livestock. Continued selection, as in the past, must be maintained to keep the stocks both from deteriorating and to enhance useful mutants. Provided that lop-sided selection is not widely practiced or taken to an extreme the disadvantages of correlated responses will not be felt.

#### SUMMARY

Mather's theory of correlated responses postulates that selection for a normally balanced, polygenically controlled character produces unusual recombinants from crossing-over. Other changes occur, and variations in other characters thus released, owing to mingling of different polygenes along the chromosomes. Animal and plant breeding selection experiments showing correlated responses are analyzed in the light of this theory.

Selection for (1) the hooded pattern in rats led to sterility; (2) high and low body weights in mice produced psychological, morphological and physiological differences; (3) resistance to tumor formation in mice, following methylcholanthrene injections, led to a kaleidoscope shift in types of induced tumors; (4) high and low abdominal bristle number in *Drosophila*

produced changes in other bristles, in spermathecae pigmentation, and in mating behavior. There was gradual reduction in fertility as selection proceeded.

Selection for: (1) high and low oil content in maize produced morphological and agronomic differences, and became hindered by decreased fertility; (2) earliness and cold tolerance in sweet corn led to pseudo-starchiness; (3) pleiocotyly in outbreeding species produced correlated changes in vigor, morphology and disturbances in hormonal balance, and increased lethality. Inbreeding species so far have shown no correlated responses. The transformation of pneumococcal types and changes in viruses during their passage through plants are also related to the theory.

Some evolutionary aspects of correlated heredity are discussed. Extinction of some animal and plant species may have occurred by specialized selection bringing about correlated loss of fertility. An evaluation is outlined of correlated responses in plant breeding, especially for pleiocotyly selection. Their disadvantages will not be felt providing lop-sided selection is not practiced to an extreme.

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CYTOLOGY OF THE GRASSHOPPER GENUS *CIRCOTETTIX*

W. L. EVANS

University of Texas

## INTRODUCTION

This paper deals with the occurrence of heteromorphic chromosome pairs, supernumerary chromosomes, and an intraspecies hybrid in the grasshopper genus *Circotettix* (Acrididae, Oedopodinae), the behavior of the chromosomes at meiosis and their distribution in the populations. Forty-six individuals of *C. undulatus*, 68 of *C. rabula*, 7 of *C. coconino*, and 7 of *C. crotalum* have been examined. These, with *C. verruculatus* which has been extensively studied by others, constitute five of the eight species of the genus described by Rehn (1921).

The first cytological observation of the genus was reported by Carothers (1917), who studied eleven individuals of *C. lobatus* (= *undulatus*), and one of *C. rabula*. She showed through the use of heteromorphic homologous chromosomes that segregation is at random in the first meiotic division. *C. verruculatus* was used by Carothers (1921) in breeding experiments to observe the behavior of the three pairs of asymmetrical bivalents cytologically.

Following this, some cytological work on females of *C. verruculatus* was reported by McNabb (1928).

The following year, Helwig (1929) published a statistical study on 295 males of *C. verruculatus* collected from localities in New England and Michigan. Of the ten bivalents present in first metaphase, four were invariably metacentric (V- or J-shaped), three were always acrocentric (rod-like), with the remaining three either homozygous metacentric, homozygous acrocentric, or structurally heterozygous, i.e., consisting of one metacentric and one acrocentric chromosome. The X-chromosome was always metacentric as is the case in all species of *Circotettix* which have been studied.

*C. verruculatus* was also used by Helwig (1933, 1938) for studying the cytological effects of irradiation. There seems to be little correlation between the chromosomal aberrations produced by X-rays and the heteromorphic bivalents found in the natural populations. The fact that the centromere (spindle fiber attachment) regions were more susceptible to breakage lends possible support for occurrence of centric fusions and centric shifts in the wild populations of these and certain other grasshoppers.

More recent work on the genus is that of White (1949) who examined 21 individuals of *C. crotalum* cytologically and one individual each of *C. undulatus*, *C. coconino*, and *C. rabula altior*. All of these had the typical cytological composition found in males of the genus, i.e., 21 chromosomes, some of the autosomes were metacentric, some acrocentric, but the X-chromosome was always metacentric. The genus is regarded by White as closely related to section B of the genus *Trimerotropis*, being probably a montane derivative of it.

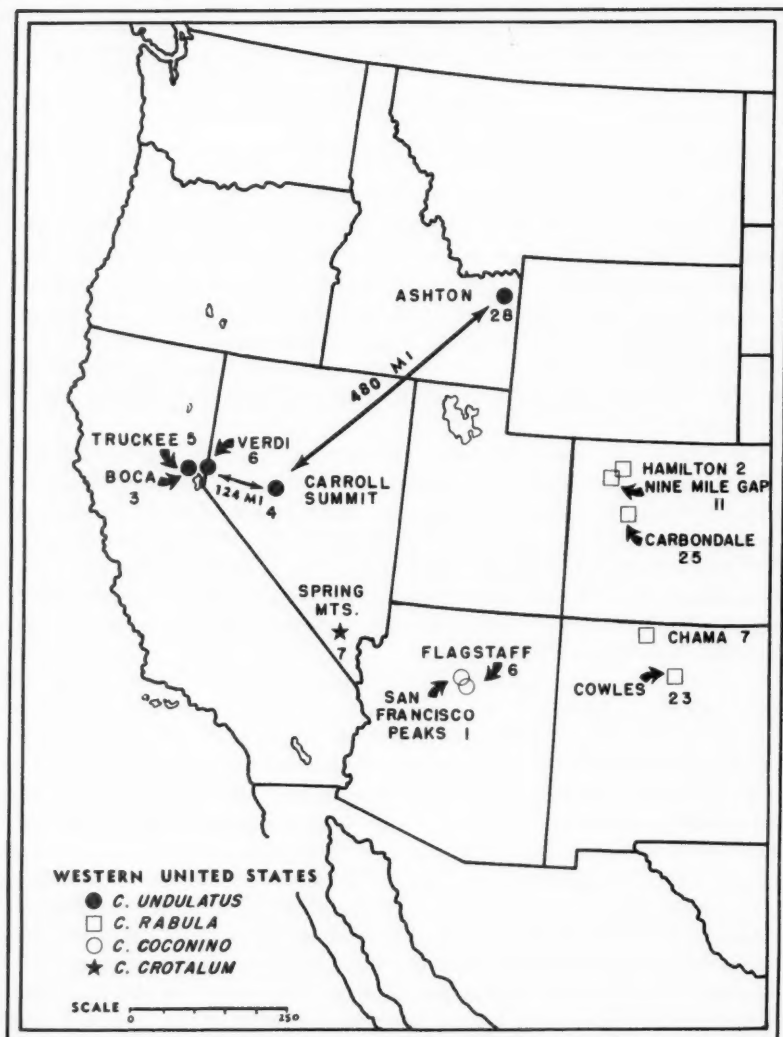


FIGURE 1. The collecting localities. The number with each locality indicates the number of individuals analyzed.

The geographical localities of the populations which are considered here are shown on the map (fig. 1). *C. undulatus* is represented by material from three distinct populations, each separated from the others by a large distance. In *C. rabula*, the two races *C. rabula rabula* and *C. rabula altior*, as well as some of the intermediates, are represented in the material but are not considered separately because of the variable amount of intergradation which

occurs in southern Colorado and northern New Mexico. Testes were fixed in San Felice's fixative, sectioned at 22 and 26 micra, and stained using Newton's Gentian Violet Method.

## CYTOLOGICAL OBSERVATIONS

*Circotettix undulatus*: Of a total of 46 individuals analyzed, 28 are from Ashton, Idaho, 4 from Carroll Summit, Nevada, and a third population on the California-Nevada border is represented by 14, 6 were collected at Verdi, Nevada, 5 at Truckee, California, and 3 at Boca, California.

Cytological examination of the material from Ashton and Carroll Summit shows only two bivalents in the first metaphase which are heteromorphic. One of these is a large chromosome pair (fig. 2A) and the other is the smallest pair (fig. 2B). In these two populations, four bivalents are always homozygous metacentric and four are always homozygous acrocentric. The frequency of occurrence of the large pair in heterozygous condition is lower (7.1 per cent of the Ashton population) than that of the small pair. Both of these chromosome pairs occur in homozygous metacentric and homozygous acrocentric condition; however, the relative frequencies of these are different.

Supernumerary chromosomes are sometimes present in *C. undulatus* (table 1). One individual from Verdi has one supernumerary. Five of the individuals, or 17.9 per cent from the Ashton collection, have one supernumerary chromosome present; two have two supernumeraries (7.1 per cent), while one possesses three supernumerary chromosomes (3.6 per cent). Carroll (1920)

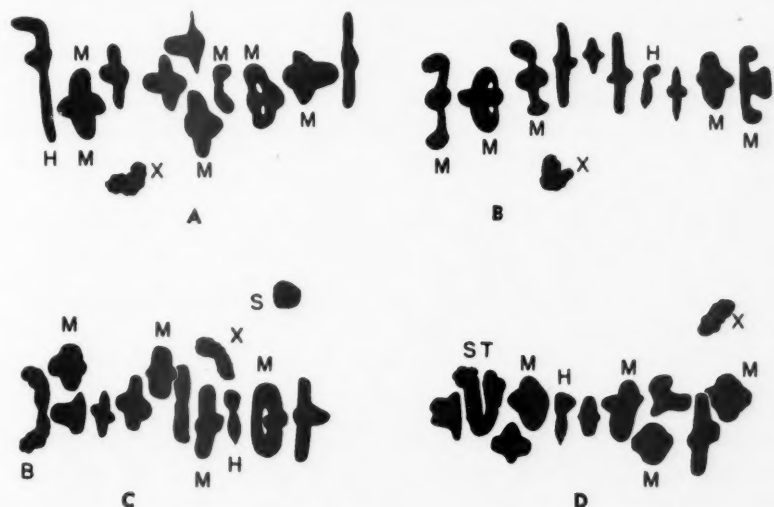


FIGURE 2. *Circotettix undulatus*. A. First metaphase with a large heterozygous bivalent (H); B. First metaphase in an individual with five metacentric bivalents (M); the smallest bivalent is heterozygous (H); C. First metaphase in which three supernumerary chromosomes are present; two forming a bivalent (B) while the third (S) is near the pole; D. First metaphase; supernumeraries form a trivalent (ST).

TABLE 1  
SUPERNUMERARY CHROMOSOMES IN TWO SPECIES\*

Species	Locality	No. Analyzed	No. Individuals with		
			1 Sup.	2 Sup.	3 Sup.
<i>C. undulatus</i>	Ashton, Ida.	28	5	2	1
	Verdi, Nev.	6	1	....	....
<i>C. rabula</i>	Cowles, N.M.	23	3	1	....
	Nine Mile Gap, Colo.	11	1	....	....

\*No supernumeraries were observed in either *C. coconino* or *C. crotalum*.

reported three supernumerary chromosomes in *Cammula pellucida*; however, only two of these synapsed, the third lying free in the region of the pole. *Trimerotropis sparsa* and *T. suffusa* also have three supernumeraries in some individuals (White, 1951c).

The supernumerary chromosomes are positively heteropycnotic in diplotene and diakinesis but do not differ in appearance from euchromatic material in the first metaphase, except in those cells in which two or three have synapsed and are arranged together on the spindle in the form of a bivalent or trivalent. The supernumerary bivalent or trivalent is recognized easily because of negative heteropycnosis similar to that of the X-chromosome (fig. 2C and 2D). In males possessing two supernumeraries, the frequency of pairing is 42.0 per cent.

In the individual with three supernumerary chromosomes, two are metacentric; the third is acrocentric. These are not distinguishable in the spermatogonial metaphase from the autosomes. Sixty-three cells from four cysts were checked and of these, 77.8 per cent contain supernumerary bivalents formed by the two metacentric supernumeraries, 12.7 per cent contain a supernumerary trivalent, and the remaining 9.5 per cent have the three supernumeraries independent of each other.

The material from Verdi, Truckee, and Boca represents a single population because of the proximity of the three localities. Three distinct chromosomal types are present in this California-Nevada border population. The first has the typical chromosome number found throughout the genus, *i.e.*, 20 autosomes and an X-chromosome.

The largest bivalent is always metacentric in this group and has apparently resulted from a centric fusion, *i.e.*, two acrocentric chromosomes have become permanently fused in the region near the centromere. In this group, the second, third, and fourth bivalents are invariably metacentric, while four bivalents are always homozygous acrocentric. Two bivalents are variable, being present in all three forms, homozygous metacentric, homozygous acrocentric, and heterozygous.

In the second chromosomal type, 23 chromosomes are present, so that 11 bivalents are formed in first metaphase. The extra chromosome pair has been designated  $1_L$  for identification purposes and is always homozygous acrocentric.

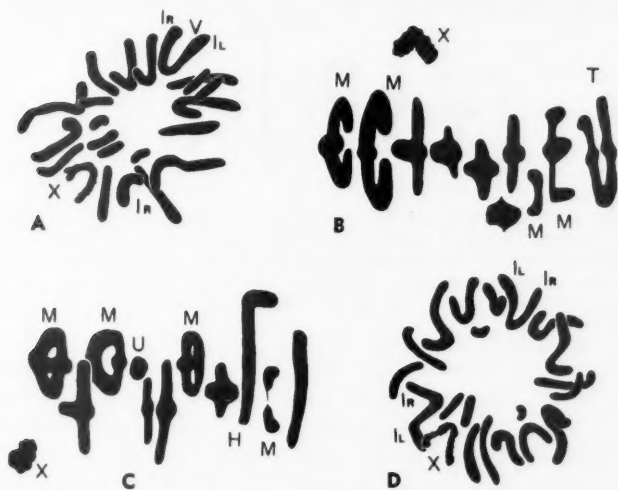


FIGURE 3. *Circotettix undulatus*. A. Spermatogonial metaphase; the fusion metacentric (V) is present, and  $l_R$  indicates the smaller J-shaped chromosome which enters into formation of the trivalent; B. First metaphase in a 22-chromosome hybrid with a trivalent (T); C. First metaphase in a 22-chromosome hybrid with an asymmetrical bivalent (H) and a univalent (U); D. Spermatogonial metaphase in which two fusion metacentric chromosomes ( $l_R l_L$ ) are present.

The third chromosomal type has only 22 chromosomes (fig. 3) and is a natural hybrid between the 21-chromosome type and the 23-chromosome type. Three of the chromosomes are of particular interest. One is the very large fusion metacentric ( $l_R l_L$ ) seen paired as a bivalent in the 21-chromosome type. This metacentric chromosome possesses equal or almost equal arms. The second is an acrocentric chromosome ( $l_L$ ) which is homologous to one arm of the large metacentric chromosome ( $l_R l_L$ ). The third is a small J-shaped autosome which is homologous to the other arm of the fusion metacentric. In first metaphase, these three chromosomes either form a trivalent (fig. 3B) or, in a relatively small percentage of cells (15.5 per cent), the J-shaped chromosome ( $l_R$ ) remains free as a univalent while the large metacentric and the acrocentric chromosomes form an asymmetrical bivalent (fig. 3C). The two acrocentric chromosomes which apparently have fused to form the fusion metacentric ( $l_R l_L$ ) exist unaltered in one of the 23-chromosome individuals; thus in first metaphase, two homozygous acrocentric bivalents are present instead of a metacentric bivalent. In all the cells in which the trivalent was present, typical configurations shown in the composite drawing (fig. 4) were seen.

A total of four individuals from the collection show the trivalent, but only three of these are sufficiently good material so that the orientation of the three autosomes could be checked accurately. White (1951b) reported a trivalent in one individual of *Trimerotropis sparsa*; however, too few first meiotic divisions were present to check orientation of the chromosomes.

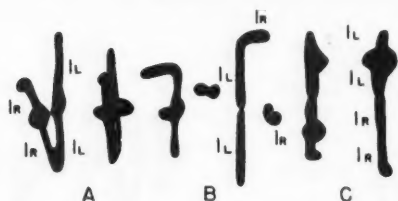


FIGURE 4. Composite drawing indicating the orientation of the three chromosomes which sometimes form a trivalent in 22-chromosome hybrids of *Circotettix undulatus*. A. Trivalent is oriented on the spindle so that disjunction is normal; B. Orientation of the three chromosomes as a bivalent and univalent; C. Orientation with the trivalent I-shaped, resulting in non-disjunction in all the cells containing this configuration.

The trivalent in *C. undulatus* is oriented on the spindle in two ways. The first of these, giving a V-shaped appearance bearing a crook on one end (fig. 4A), is present in 62.9 per cent of 116 cells counted (table 2). The second type of orientation, in which the whole trivalent is stretched on the spindle (fig. 4C), is present in 21.6 per cent of the cells and could be expected to lead to non-disjunction in every case. The third orientation results in an asymmetrical bivalent involving the large fusion metacentric ( $l_R l_L$ ) and the acrocentric chromosome ( $l_L$ ) and a univalent formed by the J-shaped element (fig. 4B). This orientation occurs in 15.5 per cent of the cells (table 2) and can be expected to lead to non-disjunction in half of these cells (7.25 per cent). Non-disjunction in these 22-chromosome hybrids can therefore be expected to reach a frequency of about 28.85 per cent as a result of these latter two forms of orientation. A fourth orientation which was expected but not encountered was that of an asymmetrical bivalent formed by the large metacentric chromosome and the J-shaped chromosome with the acrocentric present as a univalent. The absence of this type of orientation is not explained.

In this species, the same heteropycnotic bivalent at diplotene which was reported by White (1949) was present in the California-Nevada sample but not in that from Ashton. The occurrence of polyploid cells in this species will be discussed later.

TABLE 2  
ORIENTATION OF THREE CHROMOSOMES IN *Circotettix undulatus*\*

Individual No.	No. of Cysts	Cells Counted	V-shaped Trivalent	I-Shaped Trivalent	Asymmetrical Bivalent and a Univalent
1	3	49	35	7	7
2	2	47	27	18	2
3	1	20	11	0	9
Total No.	6	116	73	25	18
Percentage			62.9	21.6	15.5

\*Three chromosomes which are present in the 22-chromosome hybrids of this species.



FIGURE 5. A. *Circotettix rabula*. Spermatogonial metaphase; the metacentric chromosome (Me) pairs with an acrocentric to form a heterozygous bivalent; the small pair of metacentric chromosomes lie in the center; B. *C. rabula*. First metaphase with three heterozygous bivalents (H). C. *Circotettix coconino*. First metaphase in which the smallest bivalent is asymmetrical (H); D. *C. coconino*. Spermatogonial metaphase.

*Circotettix rabula*: The three Colorado collections of *C. rabula* consist of 25 individuals from Carbondale, 12 from Nine Mile Gap, and 2 from Hamilton. The other two samples were collected in northern New Mexico, 23 individuals at Cowles and 7 at Chama.

The analysis of these samples indicates that *C. rabula* possesses the usual number of chromosomes for this genus (fig. 5A). Seven of the ten bivalents at first metaphase are invariable. The three heteromorphic bivalents are readily distinguishable as large, medium size, and small. The two smallest pairs of chromosomes usually lie in the center of the spermatogonial metaphase plate. One triple heterozygote in which all three of the variable bivalents are heteromorphic was found (fig. 5B). Two individuals from the Carbondale collection were heterozygotes for the two larger variable bivalents. The small variable bivalent occurs in heterozygous condition with one of the other two with slightly greater frequency.

Four individuals from Cowles have supernumerary chromosomes present in all of their cells (table 1). Three of them possess a single supernumerary while one has two. With the exception of the sample from Nine Mile Gap in which one individual has a single supernumerary, none were found in the other samples. The supernumerary chromosomes are all metacentric and are positively heteropycnotic in diplotene and diakinesis. At first metaphase, the supernumerary behaves in very much the same way in *C. rabula* as in some closely related species (Carothers, 1917; White, 1949), lying away from the plate area toward the region of the pole. Its behavior in this

respect resembles that of the X-chromosome except that it does not appear negatively heteropycnotic in this stage. Ordinarily, the two arms of these metacentric supernumerary chromosomes pair with each other so that the supernumerary is almost spherical. This chromosomal behavior resembling an isochromosome has been described for supernumeraries in *Trimerotropis latifasciata*, *T. sparsa* and *C. undulatus* by White (1949, 1951a). In the one individual possessing two supernumeraries, there is no differential appearance between the two supernumeraries when this pairing occurs. However, when these arms did not pair (in about 50.0 per cent of the cells), the chromosomes are negatively heteropycnotic. By second metaphase, the supernumeraries cannot be distinguished from the other metacentric chromosomes. No lagging on the spindle in first anaphase by the supernumerary such as that described by White (1949) for *C. undulatus* was observed in this species.

Another type of variation exists in only a portion of cells of four of the grasshoppers. In at least one individual from all three of the largest collections of this species, polyploid cells are present at first metaphase, and in all but a single cell, these polyploid cells are tetraploid. Usually only one or two cysts are involved, but these also contain normal diploid cells. These polyploid cells are probably the same types which were described by Hartman (1913) as giant cells, and are of two types. In the first, univalents, trivalents, quadrivalents, and in one case, more complicated figures are present in addition to the bivalents. The second type of polyploid cell has only bivalents. In all the individuals having polyploid cells degenerating heteropycnotic cells are also present. In some cases these are extremely common (in one, they were observed in nine cysts in one field). This pathological condition, however, also occurs in individuals in which no polyploid cells are present, so the presence of degenerating cells may or may not be due to the polyploid cells. From the genetical implications alone, these polyploid cells are probably of little importance since they would seem to favor degeneration rather than maturation.

*Circotettix coconino*: *C. coconino* was collected in the vicinity of Flagstaff, Arizona. This species is represented by only seven individuals in this study. It is limited to the transition and lower Canadian zones in northern Arizona (Ball, *et al.*, 1942).

There are only two cytological types among the seven individuals of *C. coconino* examined. Both of these have four large pairs of metacentric chromosomes present in first metaphase, along with five pairs of acrocentric chromosomes. The only bivalent varying is the smallest, which is structurally heterozygous in one individual (fig. 5C). This smallest bivalent varies with the greatest frequency throughout all the species of *Circotettix* which have been examined. The remaining six are cytologically homozygous, being quite similar to the single male reported by White (1949).

*Circotettix crotalum*: This species is known to occur only in the Spring and Sheep Mountains in southern Nevada, having an extremely restricted distribution. The seven individuals examined represent a different population

from the material which was studied by White (1949) but show a similar cytological composition. Four of the bivalents are invariably metacentric; five are invariably acrocentric. The smallest bivalent is heterozygous in two individuals. It was not found in the homozygous acrocentric condition; however, since the acrocentric chromosome is present in the population, a certain percentage of the individuals can be expected to have this bivalent acrocentric. Such acrocentric bivalents were reported in the Hidden Forest population by White (1949).

No supernumeraries are present in the individuals of this species. *C. crotalum*, like *C. verruculatus* and *C. coconino*, is not known to possess supernumeraries. On the basis of structural heterozygosity, *C. crotalum* resembles only *C. coconino*, both having one bivalent known to vary.

#### DISCUSSION

Cytologically, the four species of *Circotettix* which have been examined in this study vary in a number of ways. Whereas these show a similar type of structural heterozygosity reported in many species (Carothers, 1913, 1917, 1921, 1931; Helwig, 1929; Coleman, 1948; White, 1949, 1951a; and others), the degree of this heteromorphism is decidedly different in some. *C. verruculatus* varies in three bivalents (Carothers, 1921; Helwig, 1929). These variable pairs may be the same or nearly the same as the three in *C. rabula*, differing only in certain genes and gene arrangements. The two smaller pairs which are present in both, one varying, are almost certainly the same bivalents, although these too may vary in genetic makeup. These two species appear to be very similar cytologically; however, Peck (1951) found only the smallest bivalent variable in a large sample of *C. rabula altior* from Cloudcroft, New Mexico.

Of the two species, *C. crotalum* and *C. coconino*, the former has been subjected to a more thorough examination (White, 1949); however, both so far as is known have only one variable bivalent. In both these species, four large chromosome pairs are always metacentric with the remaining ones acrocentric. Thus, these two southwestern species appear quite similar.

*C. undulatus* is cytologically the most complex of the species of *Circotettix* considered to this time. Samples from two populations show the usual 21 chromosomes which form two variable and eight symmetrical bivalents in first metaphase. However, the California-Nevada border sample indicates that 22 and 23 chromosomes can be present in males without supernumerary elements being involved. Several possible explanations can account for this unusual condition.

On the basis of evidence by White (1945, 1949), a complex of 23 chromosomes is the ancestral condition of *Circotettix*. One fusion of two acrocentrics resulted in 21 chromosomes, the basic number found in all of the species of known cytological composition. The other metacentrics have arisen by centromere shifts or other rearrangements, possibly inversions. In the 21-chromosome type, the fusion metacentric is present in homozygous condition along with four pairs of metacentrics which have arisen through

centromere transposition. The 23-chromosome individuals have the ancestral number of chromosomes. The 22-chromosome individuals with the trivalent are natural hybrids between these two chromosomal types, the large fusion metacentric being derived from one parent while the acrocentric homologue of one arm and the J-shaped homologue of the other is derived from the other parent. There is no evidence that a pure 23-chromosome "race" of *C. undulatus* exists anywhere. The population in which the 22 and 23 chromosomes are found is on the extreme edge of the distribution area of this species and may be the only one in which the ancestral number of chromosomes is still present.

A second alternative is that breakage of the fusion metacentric in the 21-chromosome type resulted in two rod-shaped chromosomes, again producing the ancestral number. For these to remain in the population would necessitate the acquisition of a centromere by one, possibly from a supernumerary. Although this possibility has long been considered highly improbable, Ward (1949) reported the presence of 14 chromosomes in several males of *Drosophila trispina*, showing an increase in the number of chromosomes over that which is considered basic for the genus.

The condition in the border population of *C. undulatus* may be due to some "introgression" from *C. thalassinus*, a closely related species occurring in California relatively near and possibly overlapping the area inhabited by *C. undulatus*. One individual had 11 pairs of autosomes, an X-chromosome, and a supernumerary (personal communication from M. J. D. White). Such relationship with *C. thalassinus* can neither be verified nor refuted until the cytology is thoroughly known.

A third type of variation found in the genus *Circotettix* is restricted to only two species thus far examined. Both *C. undulatus* and *C. rabula* have supernumerary chromosomes in some individuals. The relative frequencies of these supernumeraries vary markedly in the two species. Whereas *C. undulatus* has supernumeraries present in 19.3 per cent of the individuals examined, *C. rabula* contains these supernumeraries in only 7.5 per cent of the individuals. The reason for this wide variation may rest with the populations studied. In the sample of *C. rabula* from Carbondale, Colorado, no supernumeraries were found, while in another sample collected at Cowles, New Mexico, a total of five supernumeraries was observed. It is probable that whereas these supernumeraries are widespread, being found both in Colorado and in New Mexico, some populations can be found in which supernumerary chromosomes are lacking. This may be significant, if supernumeraries act genetically to increase or decrease viability (White, 1951a). A contrasting picture is present in *C. undulatus* in that the frequency of the supernumeraries in the Ashton population is the highest which was encountered. It seems that supernumeraries in closely related species or even in the same species do not always behave alike. In *Trimerotropis sparsa* when two metacentric supernumeraries are present, they rarely form a bivalent (White, 1951a); however, in *C. undulatus* bivalents are formed in 42.0 per cent of the first meiotic divisions.

The fact that supernumeraries have not been found in *C. coconino* and *C. crotalum* may be due to the small samples examined, samples from too few localities have been considered, or supernumeraries do not exist in these species.

It is in these latter two species that the least structural heterozygosity was noted; however, since no supernumeraries have been reported present in *C. verruculatus*, there may be no correlation between these two phenomena. On the other hand, at least some of the supernumeraries have probably arisen in the course of evolution as a result of the formation of a fusion metacentric, where one centromere with the adjacent heterochromatic region became disjoined from the rest of the chromosome and remained present as a supernumerary.

Like supernumeraries, polyploid cells have been observed only in *C. undulatus* and *C. rabula*. These are formed by fusion of diploid cells as well as a result of cytokinesis being suppressed. Helwig (1933) reported an abundance of such polyploid cells resulting from the latter cause. The presence of these polyploid cells probably exerts little if any genetic effect on the populations in which they are found, resulting only in a reduction of the number of gametes formed.

#### SUMMARY

Four distinct types of cytological variation are present in the species of *Circotettix* which have been examined.

1. Asymmetrical bivalents consisting of a metacentric and an acrocentric homologue are present in all four species. *C. rabula* and some of the material of *C. undulatus* have three variable bivalents. *C. coconino* and *C. crotalum* vary in only the smallest bivalent.

2. Supernumerary chromosomes are present in *C. undulatus* and *C. rabula*. Three is the maximum number seen in *C. undulatus* and two in *C. rabula*. In individuals with two supernumerary chromosomes, the supernumeraries form bivalents in some cells and remain independent in others. In the individual with three, supernumerary trivalents, bivalents and univalents are present.

3. Based on the cytology in the males, 21- and 23-chromosome types are present in *C. undulatus*, and a 22-chromosome hybrid is formed when the two types cross. This condition occurs on the edge of the distribution area.

4. Polyploid cells occur in a number of individuals of *C. undulatus* and *C. rabula*; however, evidence is presented that these result from pathological conditions and are of little if any genetic significance.

#### ACKNOWLEDGMENTS

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## $Q_{10}$ AS A FUNCTION OF SIZE AND HABITAT TEMPERATURE IN POIKILOTHERMS<sup>1</sup>

K. PAMPAPATHI RAO<sup>2</sup> AND THEODORE H. BULLOCK

Department of Zoology, University of California, Los Angeles

A number of recent studies have been concerned with compensatory mechanisms by which poikilotherms adapt themselves to habitats of different temperatures, for example, different latitudes (Bullock, 1951; Roberts, 1952; Scholander et al., 1953; Rao, 1953). It is agreed by these authors and was already well documented years ago (Mayer, 1914; Edwards and Irving, 1943a and others) that at least some species, when cold-acclimated or -adapted, show higher metabolic rates (or other rate functions) at any given temperature, within limits, than when warm-acclimated or -adapted.<sup>3</sup> Scholander and coauthors (1953) have recently contributed, in a most valuable paper, a wealth of measurements of metabolism in arctic and tropical poikilotherms, representing by far the greatest documentation of rate functions to date in animals of *different* species adapted to widely differing temperatures. However, Scholander and coauthors find no role for alteration of the sensitivity of metabolism to temperature change, measured by  $Q_{10}$ , in the climatic adaptation of poikilotherms. They furthermore consider that because the effect of size, assuming a regression of about 0.8, is often smaller than the total scatter, it need not be taken into account in the rate-temperature plots. (The regression coefficient is an exponent by which body weight is raised to give a figure regarded as proportional to metabolism.)

Both of these conclusions are at variance with the results of a variety of investigations in this laboratory on intraspecific comparisons. Accurate determination of these slopes depends on reducing the scatter of points to a minimum. Among several other factors which contribute to the scatter (e.g., activity, nutritional status, large gonads, tidal rhythm) we have found size to be important. This is not only because larger individuals exhibit lower activity per gram for most rate functions, but also because there is a different influence of temperature on activity in small versus large members of a species.

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<sup>2</sup>Present address: Department of Zoology, Andhra University, Waltair, India.

<sup>3</sup>Conforming to the usage of some previous authors, we will call those regulatory modifications occurring during the life of the individual acclimation and those manifested by separate populations, which could be genetic, acclimatization. Adaptation includes the latter but may also be merely changes in tolerance without regulation of rate in non-extreme temperatures.

## EFFECT OF SIZE

The recent statement by Bishop (1950, p. 242), to the effect that smaller individuals of a species respond to temperature changes more markedly than do larger ones is widely believed. It appears to be based on the data of Edwards (1946) and on erroneous reading of graphs for *Melanotus* and *Talorchestia*. Replotting these graphs logarithmically, weight against rate, or semi-logarithmically, rate against temperature, shows that they give evidence for some increase in response with size. A number of examples demonstrating increasing temperature coefficients with age or developmental stage, in a variety of physiological activities have been gathered together by Bělehrádek (1930, 1935; respiration, development, heart rate). There are some cases of the opposite (decreasing coefficients with age), and some opinions that no regular change in temperature coefficients is associated with age, but the weight of evidence clearly indicated that there is frequently some systematic progression of coefficients in development and that this is usually in the direction of increase. Consequently it seemed desirable to re-examine available evidence.

We have accordingly calculated the  $Q_{10}$ <sup>4</sup> for the various size<sup>5</sup> groups from each of the recent studies offering the necessary data. The amphipod, *Talorchestia*, from the data of Edwards and Irving (1943b) shows increasing  $Q_{10}$  with size (indicated by a decreasing weight regression at higher temperature) between 12° and 22° C in summer animals (figures 1 and 3). Winter animals show the contrary but the temperature range used suggests that the summer animals are less likely to show cold depression at 12° in large individuals than the winter ones are to show heat depression at 22° in large individuals. The case is not a strong argument because of the limited number of points but the interpretation suggested is strengthened by curves presented in a later paper—without points (Edwards, 1946), in which slopes for winter animals at additional temperatures are given. Between 7° and 17°  $Q_{10}$  increases with size but at 23° and 32° the very steep regression lines indicate heat depression of large sizes.

Similarly *Emerita*, an anomuran sand crab, shows increasing  $Q_{10}$  with size above 500 mgms and between 16° and 21° C or 16° and 26° C but not between 21° and 26° C (Edwards and Irving, 1943a, replotted in figures 2 and 3). The beetle, *Melanotus* (Edwards, 1946) shows a slightly

<sup>4</sup> Although the authors in agreement with Scholander et al. prefer to use the arbitrary expression of temperature response,  $Q_{10}$ , the expression  $\mu$  value may be substituted wherever the former is used in this paper except when values for  $Q_{10}$  are given. We are here concerned with the fact of and the direction of alteration in temperature response, not in its magnitude which will be up to 10 per cent different between 0 and 30° C on the two systems. We prefer neither to imply a theoretical energy of activation (which is patently inappropriate in many natural and physiologic responses whose  $Q_{10}$ 's are extremely high or low) nor to ignore the empirical facts of consistent differences in temperature response because of possible misunderstanding of its bases.

<sup>5</sup> The significant factor may be physiological age but animals of the same size may be chronologically older in higher latitudes or intertidal levels so that it seems necessary to speak of the measured quantity, size.

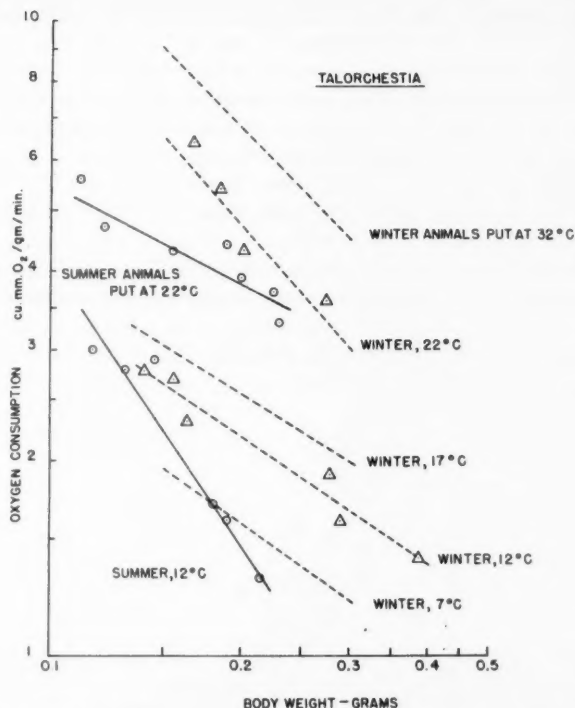


FIGURE 1. Oxygen consumption of *Talorchestia* replotted from the data of Edwards and Irving, 1943b, (solid lines and circles, dashed lines with triangles) and Edwards, 1946 (dashed lines without points). No points are given in the latter paper; faithful reploting of the straight lines given on arithmetic plots would yield the unlikely result of weight regression strongly increasing with age, therefore the straight line, log-log, through the end values is given although the comparison of slopes would not be affected if they were curves. Note that (1) summer animals, 12–22°, increase Q<sub>10</sub> with size; (2) winter animals, 7–17°, do the same but (3) in winter large animals are heat depressed at 22° and higher; (4) the metabolism of small winter animals at high temperatures is unexpectedly high, i.e., not depressed in proportion to the larger sizes; (5) at 12° winter animals are less size dependent than summer animals hence acclimated and more so in large sizes; (6) weight regression is not a characteristic figure for the species but varies with temperature and season.

increasing Q<sub>10</sub> with size (figure 3) for each pair of temperatures in the whole range of 12°–40° C (except for large individuals at 12°) but again no great weight can be given this case since no points but only smooth curves were given. While the reliability of these trends relative to the variance of the original data cannot satisfactorily be estimated, in another case, that of the rate of water propulsion by *Mytilus* (Rao, 1953) the trends are highly significant (figure 3).

Four additional cases are not plotted in the figures. The cunner, *Tautoglabrus adspersus*, given by Haugaard and Irving (1943) agrees with those above but only three animals of known weight are available. The

$Q_{10}$  of oxygen consumption of a 30 gm. fish was 1.9, of a 49 gm. fish 3.5 and of a 50 gm. fish 2.2, all between  $21^{\circ}$  and  $26^{\circ}$  C. These data are too few to give the present argument any real support but they are in the same sense and not contrary to it. This is the situation for much of the scattered data we can find in which rate functions at various temperatures are measured and fragmentary indications of size are given.

The crab, *Pachygrapsus crassipes*, was shown by Roberts (1952) to have a reliable increase in  $Q_{10}$  with size in the range  $16^{\circ}$ – $23.5^{\circ}$  C but no trend between  $8^{\circ}$  and  $16^{\circ}$  C.

Vernberg (1952) gives data for two species of salamanders permitting the calculation of  $Q_{10}$  from eye-fitted curves (only two temperatures). Larger

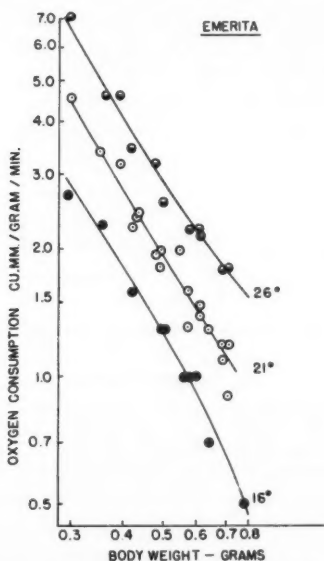


FIGURE 2. Oxygen consumption of *Emerita*, replotted from the data of Edwards and Irving, 1943a (p. 178, summer animals). Note that size regression is greater at  $16^{\circ}$  than at higher temperatures, at least in large animals.

sizes consistently show higher quotients; thus 0.85 g. *Eurycea* (Oct.–Nov.) have a  $Q_{10}$  ( $1^{\circ}$ – $10^{\circ}$  C) of 3.4, 1.4 g. specimens, 3.7; and 0.55 g. *Plethodon* similarly measured yield a  $Q_{10}$  of 1.8 while 0.9 g. specimens give a value of 3.0.

The data of Wells (1935) on the metabolism of *Fundulus* argue on the whole against an increasing  $Q_{10}$  with size but the results are inconsistent. Calculated from his table II, pp. 209–210, we find the  $Q_{10}$  ( $10^{\circ}$ – $22^{\circ}$  C) decreased with increasing size in two experiments (in Exp. 3 from 3.6 to 1.8 for fish of 2.2–2.4 and 6.3–6.6 gms., respectively, and from 3.1 to 2.2 for the same fish in Exp. 4) but increased slightly in a third case (2.7 to 2.8 for the same specimens in Exp. 5). Furthermore, Wells emphasizes the

occurrence of sudden breaks at several temperatures in all series and the probable peculiarities of 2-5 gm. *Fundulus*. Further data on this and other fish would be valuable, especially if a physiological temperature range is assured, within which the  $Q_{10}$  is shown to be nearly uniform and a number of size groups is used.

The range of points on the graphs of metabolism against temperature in figures 7 to 12 in Scholander et al. (1953) cannot be regarded as entirely random scatter, since the individuals in most species varied greatly in size. Assuming as an approximation that the points at the upper end of the scatter (higher metabolism per gram) belong to the smaller animals and those at the lower end to the larger individuals, one can draw slopes through the upper and lower regions of the scatter plots. (Note that no assumption has to be made as to the magnitude of the size regression but only that there is one as is well established generally for cold-blooded

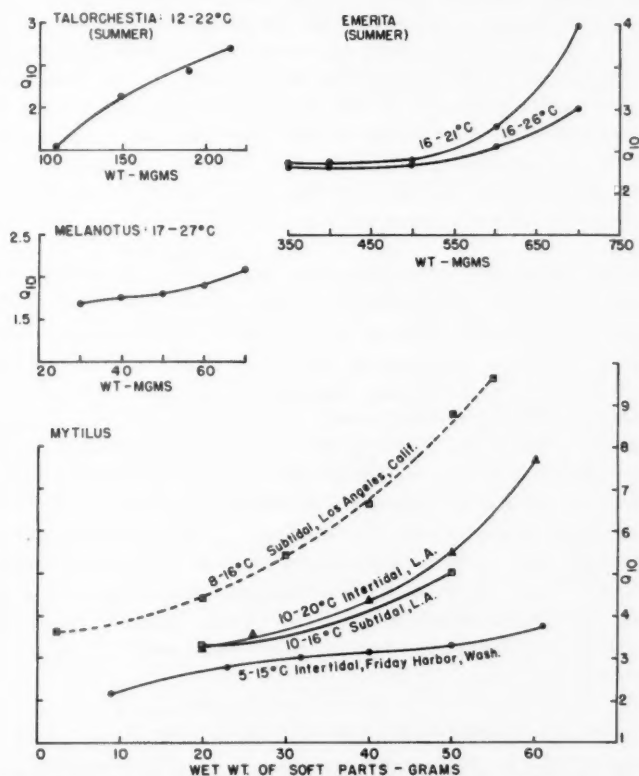


FIGURE 3.  $Q_{10}$  as a function of size. For *Mytilus californianus*  $Q_{10}$  values presented are for the rate of water propulsion. In the rest of the cases the values refer to the rate of oxygen consumption. *Talorchestia*, from summer curves figure 1 *Emerita* from figure 2. *Melanotus* calculated from Edwards (1946). *Mytilus* partly from Rao (1953), partly original.

animals. The other assumption involved is that all other causes of scatter together are not systematically and inversely correlated with temperature.) A flatter slope for the upper region indicates a lower  $Q_{10}$  in smaller individuals, while parallel slopes indicate no change in  $Q_{10}$  with size. Of the 36 cases plotted by the above authors, twenty-four show a higher  $Q_{10}$  for the presumably larger sizes, while in nine cases there is no apparent difference in the slopes.

Only three cases (namely, the tropical flesh fly, the arctic fairy shrimp, and the arctic land snail) show any indication of a decreasing  $Q_{10}$  with increasing size. The arctic spider crab, near the upper end of the temperature range, shows a similar trend. Likewise, the arctic slug shows the same phenomenon between 10–20° C, while it conforms with the majority of the cases over the temperature range 0–10° C and 20–30° C. All of the cases where there is no apparent change of  $Q_{10}$  with size are tropical with the exception of the arctic Brown fly. In nearly all these cases there may be noticed a distinctly greater slope for the presumably larger individuals, between 20 and 30° C, indicating an increasing  $Q_{10}$  with size within this temperature range. In the case of the arctic Brown fly the same phenomenon may be noticed between 0 and 10° C. Amongst the exceptions the arctic fairy shrimp is represented by only three animals. The arctic land snail shows an increasing  $Q_{10}$  with size between 10° and 20° C, while below this range it is just the opposite. The fact that the water in the pond, where the animals were collected, was 14° C at the time may be significant.

The weight of evidence from this paper then is in favor of a common increase of temperature coefficient with size, on the specified assumption of a weight regression—which quite possibly is not always true (Vernberg and Gray, 1953) but is probably the case in most of the species concerned as the plots of weight against rate (figures 1–5) indicate.

However, we would emphasize that it is not the contention of this communication that the increase of  $Q_{10}$  with size and with habitat temperature, although regarded as usual, is general either among species or for all sizes or temperature ranges. Temperature response is a complex function and in many respects varies among animals (e.g.  $Q_{10}$  as a function of temperature measured acutely over a wide range) so that we are recognizing common trends rather than rules at this stage of refinement. Exceptions to the usual size relation are known (Bělehrádek, 1930, 1935, Sumner and Lanham, 1942) and more may be expected but they would appear to be relatively uncommon.

#### EFFECT OF HABITAT TEMPERATURE

Turning to the question of  $Q_{10}$  and the temperature to which the animal is adapted, Bělehrádek (1935) has already pointed out that temperature coefficients commonly increase with the adaptation of the protoplasm to higher temperatures. He illustrated this by examples taken from the data

of various investigators, on the germination of seeds, production of  $\text{CO}_2$ , velocity of amoeboid movement, heartbeat frequency, cellular division, cleavage of eggs, embryonic development, the life cycle in cladocerans and locomotion in ants and his cases aggregate very weighty evidence that  $Q_{10}$  varies commonly, not invariably, with this factor.

Relative to the change of  $Q_{10}$  with acclimation temperature, the data on *Mytilus* emphasize the importance of the choice of temperature range. New data on a population of *Mytilus* from about 30 feet below low tide show that all  $Q_{10}$ 's for the same individuals are markedly displaced upwards (figure 3) when rates at  $8^\circ$  and  $16^\circ\text{C}$  are chosen instead of 10 and  $16^\circ\text{C}$  for the calculation, i.e., the  $Q_{10}$  between  $8^\circ$  and  $10^\circ$  is very high. The original data

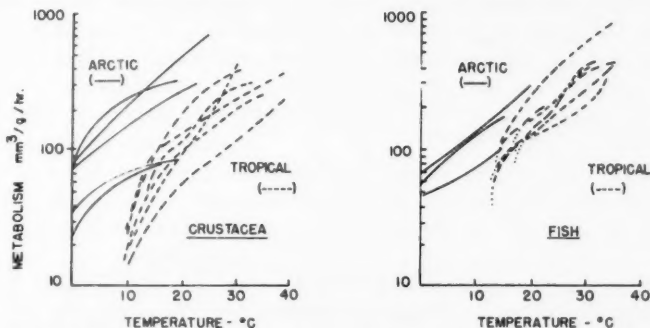


FIGURE 4. Eye-fitted curves through the scatter plots of the separate species given by Scholander et al. (1953, omitting only the stickle-back). Dotted lines slope toward lethal temperatures. Note that there is no acclimatization at higher temperatures, i.e., metabolism is the same in arctic and tropical species, roughly. But at low temperatures, arctic metabolism is higher, due to a lower  $Q_{10}$  (flatter slope), up to  $10^\circ$  difference exhibited on a horizontal line through a given rate of metabolism. Further, note that the slope ( $Q_{10}$ ) is not only generally less for arctic species at any given temperature, but even at the lower temperature for any given metabolic rate. In many species there is no significant difference comparing the supposed habitat temperatures, i.e., the acclimatization is incomplete, but in some the difference is present even at these widely separated temperatures (See figure 5).

show a sudden cold depression below  $10^\circ\text{C}$  presumably related in some way to the "physiological" range in their natural habitat. The trend with size is shown, however, in both ranges.

If we choose a range over which  $Q_{10}$  is nearly uniform (only done readily by plotting a number of points semi-logarithmically), or if we compare  $Q_{10}$ 's at temperatures giving equal rates, we find significantly lower  $Q_{10}$ 's and lower size dependence for populations from high latitude (Rao, 1953) and from subtidal habitats than for populations from lower latitudes and higher intertidal levels (figure 3). Like the size relation, this agrees with most earlier data.

In addition to Bělehrádek's cases, mention might be made of the following. Mayer (1914) gives pulsation rates for the medusa, *Aurellia aurita* at

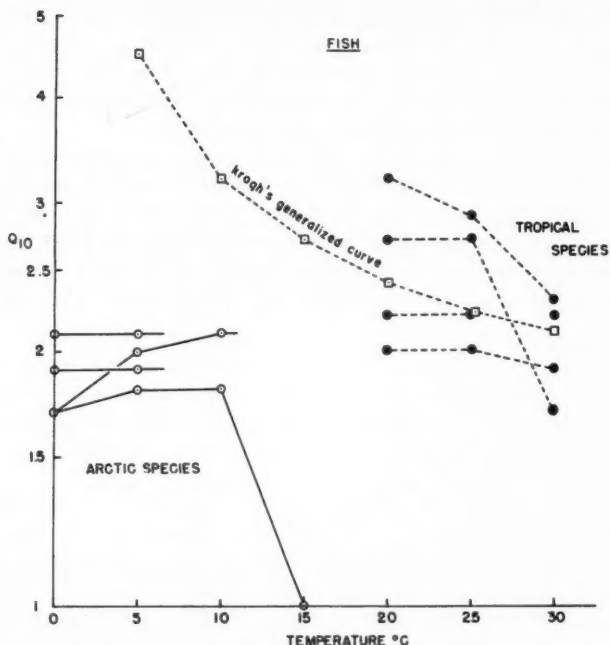


FIGURE 5.  $Q_{10}$  at probable normal habitat temperatures in arctic and tropic fish (species and data from Scholander et al., 1953, omitting the stickleback). Temperatures of equal metabolism are not so far apart and  $Q_{10}$  differences are therefore even greater. The comparisons are only valid to the extent that size is not systematically different in the two groups. This is very roughly true.

Halifax, Nova Scotia, and at Tortugas, Florida. If we compare the mid-region of the temperature range in the two localities (5–15°C in the north and 25–29°C in the south), the  $Q_{10}$ 's are 1.07 and 1.25 respectively. Peiss and Field (1950) reported a lower  $Q_{10}$  for oxygen consumption of liver slices and brain mince of the polar cod, *Boreogadus saida*, than of a temperate zone fish, the golden orfe, *Idus melanotus*. The same relation holds in summer vs. winter individuals from a Massachusetts population of *Emerita* (Edwards and Irving, 1943a, Scholander et al., 1953, table 6), at least below 16°C. This difference is very reliable.

Talorchestia (figure 1) shows an over-all acclimation in winter vs. summer samples of the same population, contrary to the conclusions of the authors (Edwards and Irving, 1943b, Edwards, 1946) who did not take into account that their winter samples averaged larger in size. The acclimation measured at 22° drops to nothing in large sizes presumably because of heat depression of winter forms and at 12° acclimation is absent in small sizes for it is inevitable that the two different slopes for weight regression must meet towards the left. Because of the temperature range available for summer animals,  $Q_{10}$ 's are not strictly comparable, but as the best

approximation if we compare summer 12-22° and winter 7-17°, the latter are lower, especially in larger sizes. One of the two species of salamander studied by Vernberg (1952), shows the usual decreasing Q<sub>10</sub> as the metabolic rate increases at given temperatures, with seasonal acclimation. The other species, while increasing its metabolism at 10°C through the same seasons, decreases its metabolism measured at 1°C and the Q<sub>10</sub> therefore increases. In line with the author's explanation, we may suggest that a seasonal shift in tolerance has resulted in 1°C being cold-depressing in June as in the cases of *Mytilus* and *Emerita*; a number of experimental temperatures would be valuable to insure against sudden changes in Q<sub>10</sub> between the points used.

Moore (1942) confirmed the increasing Q<sub>10</sub> with increased temperature of adaptation as between several species of *Rana*, measuring rate of development and comparing the middle of the physiological range for each species. In 1949 he clearly showed the same trend within one species, *R. pipiens*, contrasting those from northern United States with populations from southern United States and Mexico.

The conclusion to the contrary in Scholander et al. (1953), that Q<sub>10</sub> does not vary significantly with cold adaptation, may possibly be due to the grossness of comparing different species north and south and to scatter resulting from size and other factors.

Their conclusion is partly due to the poor correlation they observed between Q<sub>10</sub> and changeability of habitat temperature. "In this survey we have found no case where adaptation to temperature change has taken place by rendering the animal insensitive to such changes, i.e., by a low Q<sub>10</sub>. Hence the physiological adaptation of poikilotherms to cold lies in the lateral displacement of the MT (metabolism/temperature) curve." But a strict comparison of cold water and warm water species gives a different result. We find their data support the conclusion that Q<sub>10</sub> commonly tends to decrease in high latitudes with some exceptions; in particular most of the fresh water and terrestrial forms including the insects did not show acclimatization. The trend is not pronounced but is present in spite of the factors which tend to obscure it by increasing the scatter of calculated Q<sub>10</sub>'s, namely, the comparison of different species, the great scatter in the original measurements including the size effect within each species and the possibility of noncomparable age groups in the arctic and tropical species, and the necessary subjectivity of deriving Q<sub>10</sub>'s by eye-fitted tangents to eye-fitted curves. It is not suggested that any systematic errors exist but only that the accidents inherent in these factors increase the range of values obtained and thus hide the small systematic trend. This trend is nevertheless more often manifested than not—and rarely balanced by a difference in the opposite direction. Thus figures 4, 5 and 6 constructed from the data in tables 5 and 6 of Scholander et al., 1953, show that metabolism/temperature curves are not only laterally displaced but of different slope in the arctic and tropical species studied. Thus Q<sub>10</sub> values are not only different at any given temperature but are generally lower in the arctic

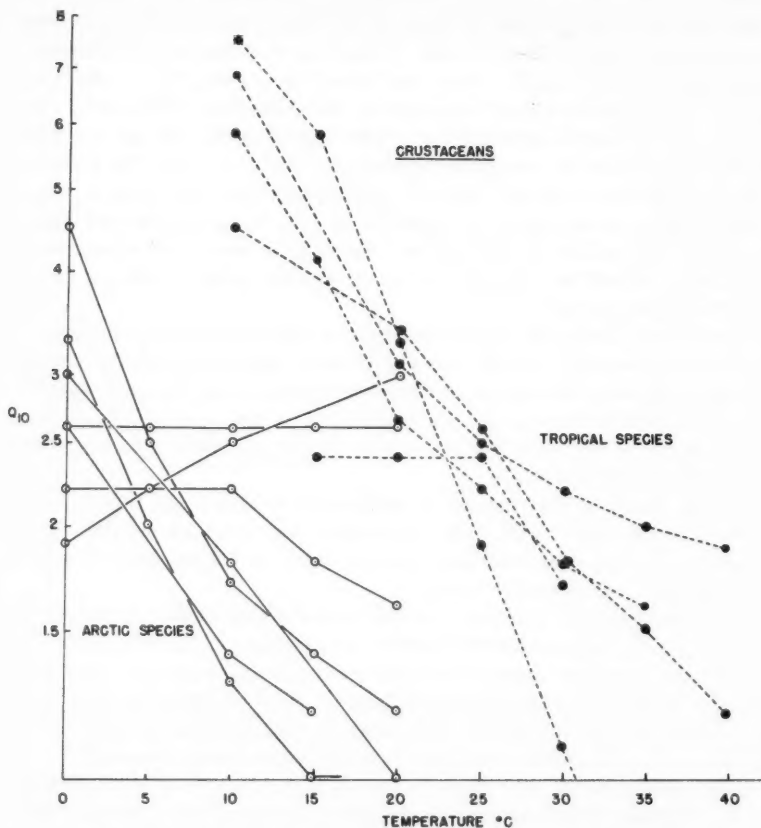


FIGURE 6.  $Q_{10}$  at different temperatures in arctic and tropical crustaceans (from Scholander et al., 1953). The difference between arctic and tropical values is great at any given temperature and is still marked at temperatures giving equal metabolism (roughly 5-10 degrees difference, below 15°C) but disappears when probable habitat temperatures are compared (about 0-5°C and 25-30°C, respectively). Some species included are very small or eurytopic or represented by few specimens.

than in the tropical species comparing at the two temperatures producing any given metabolic rate (roughly 5-10° lower in arctic forms in the range below 15 or 20°C). The latter comparison we regard as significant since it can show partial adaptation while comparison only at habitat temperatures, besides encountering the difficulty of specifying corresponding habitat temperatures, can obscure intermediate degrees of adaptation. In the usual case  $Q_{10}$  rises steeply at lower temperatures so that a large adaptation at 0-10°C would be necessary to keep it below the value at 20-30°C habitat temperature. Nevertheless this is true of most of the fishes, though not of most other species. The reliability of these differ-

ences cannot be estimated but is probably very low. We regard them as significant because they agree with the other cases where highly reliable intraspecific differences in this direction were shown. Figure 7 shows that in various intraspecific comparisons  $Q_{10}$  is lower in the forms from cooler habitats, taking temperatures of equal metabolism or water propulsion.

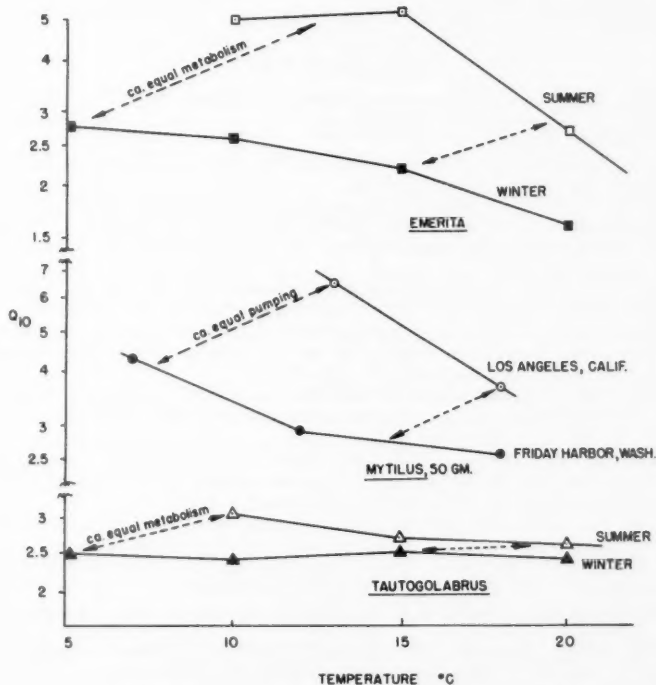


FIGURE 7.  $Q_{10}$  at various temperatures in the same species, winter vs. summer or high vs. low (temperate) latitudes. *Emerita* and *Tautogolabrus* from Scholander et al. (1953), *Mytilus* from Rao, (1953). Only the latter are size controlled. Dotted lines indicate temperatures of approximately equal metabolism or water propulsion, i.e., degree of acclimation.

These trends in the dependence of  $Q_{10}$  on size and temperature of adaptation may be real even though they may not correspond to our ideas of what would be adaptive. Scholander et al. (1953) concluded that  $Q_{10}$  was not significantly varying partly because cases which they considered as the most likely to benefit by a low  $Q_{10}$  did not consistently show it. It is natural to look for lower  $Q_{10}$ 's in animals subject to wide fluctuations in environmental temperature but as these authors point out, this correlation is poor on present evidence.

## SUMMARY

Data has been assembled from various sources, which show that  $Q_{10}$  of various measures of activity commonly increases with increasing size within the physiologically normal ranges of temperature.

Several instances are drawn together, which indicate that the  $Q_{10}$  of a given species varies with the habitat temperature to which it is adapted. Neither relation as presently formulated can be said to be necessarily adaptive and exceptions to both are pointed out.

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THE MUTAGENICITY OF FORMALDEHYDE IN DIFFERENT  
EARLY DEVELOPMENTAL STAGES OF *D.*  
*MELANOGASTER* MALES\*

IRWIN H. HERSKOWITZ

Department of Zoology, Indiana University, Bloomington, Ind.

INTRODUCTION

Although formaldehyde has so far failed to induce mutations in any stage of germ cell formation in female *Drosophila melanogaster* (Herskowitz, 1950; Auerbach, 1951a,b, 1952, 1953; Valencia, see Muller, 1951), this substance has been shown to be a potent mutagen in males of this species by a number of investigators (see Herskowitz, 1953). With the view of discovering the basis of this sex differential in mutability and of determining if certain stages in sex cell formation in males show different mutabilities to this substance, Auerbach (1951b, 1952, 1953) has studied the mutation rates obtained with formaldehyde in male germ cells in various stages of their development.

The present experiments were performed to determine germ cell mutability to formaldehyde during different early developmental stages of males. The bearings these results and others have on the problems mentioned above will be discussed briefly.

MATERIAL AND METHODS

To obtain individuals at different stages of development for treatment, a number of Oregon-R, wild-type flies were placed in bottles containing fresh culture medium for twelve hours, after which they were transferred to new bottles. This procedure was continued for eight days before the parents were discarded, at which time the last four groups of transfer bottles, used in these experiments, were treated. An aqueous solution of formaldehyde was added on top of the food of each bottle in such an amount as to produce, if the chemical substance diffused throughout the culture medium, a concentration of 0.2 per cent. Accordingly, at the time treatment with formaldehyde began, the developing individuals were 0-12, 12-24, 24-36, and 36-48 hours old, counting from the time of egg laying, in the four different groups of bottles. Random samples of  $F_1$  treated males from these groups were crossed individually to virgin females of the Basc (formerly called the "Muller-5") stock and sex-linked recessive lethal mutations in the chromosomes derived from their sperm were detected by standard methods. Up to 12 sperm were tested for mutations from each male. The entire experiment was carried out at  $25 \pm 1^\circ\text{C}$ .

\* These experiments have been supported by a grant received for work of H. J. Muller and associates from the American Cancer Society, on recommendation of the Committee on Growth of the National Research Council.

## RESULTS AND DISCUSSION

The results obtained are presented in table 1.

Although Auerbach's data led her to suggest (1951b) that formaldehyde mutations occurred only in one particular stage of male germ cell development, possibly early in meiosis, it has since then been found that formaldehyde is mutagenic when applied to spermatozoa which in one series of experiments were probably mature (Auerbach, 1952, 1953) and in another were known to be mature (Herskowitz, 1953) at the time of treatment. It was also found, when groups of larvae were given formaldehyde-treated food for one day on different days of larval life, that the highest mutation rate was obtained from larvae one day old at the time treatment began (Auerbach, 1953). This result together with others, led her to suggest that there may be a narrow zone of cells, occupying the most advanced region in the testis of young larvae, which is mutagenically the most sensitive to formaldehyde. "This condition develops only gradually during the first day; for treatment during the first 12 hours after hatching from the egg produces

TABLE 1  
MUTATION RATE INDUCED BY 0.2 PER CENT FORMALDEHYDE ADMINISTERED  
AT DIFFERENT STAGES OF DEVELOPMENT

Age in hrs. at time of treatment	Number of sex-linked lethals	Number of sperm tested	Per cent mutation	Number of males with one or more lethals			
				1	2	3	4
0-12	48	625	7.7	27	6	3	..
12-24	27	644	4.2	23	2	..	..
24-36	51	553	9.2	29	6	2	1
36-48	35	462	7.6*	16	6	1	1

\* Two suspected lethals are not included.

few, if any, mutations." (Auerbach, 1953). The high mutation rate obtained when treatment covered the entire first day of larval life must have been due then to mutations induced after the first half of this day. This relatively insensitive early period would correspond roughly to 24-36 hours from the start of development. Some support for this view may be found in the present experiments where individuals whose treatment began 12-24 hours after the start of development had a mutation rate which was statistically lower ( $P < .01$ ) than the mutation rate in individuals twelve hours older when treated (table 1). If formaldehyde-treated food, upon which larvae are feeding, loses its mutagenic effectiveness within 24 hours, as stated by Auerbach (1953), the ages which could have been treated with mutagen ranged from 12 to 48 hours after oviposition in the younger of the above two groups, and 24 to 60 hours after oviposition in the older one. These data also provide information concerning the duration of the mutagen's effectiveness. If the mutagen remained potent indefinitely, individuals 12-24 hours old when first treated could have only a mutation rate

which is greater than or equal to that in individuals 24-36 hours old when treated, depending on whether the former group is or is not mutable during its additional 12-hour period of treatment. Since however the mutation rate obtained for the former group is only about one-half that of the latter, it may be concluded that a large proportion of the mutagen decays within a 12-hour period. This means that the range of ages which could have been treated in the different groups in the present experiments have been given upper limits which are probably too high, and which when lowered would make more valid the comparison of the present data with Auerbach's.

In the earliest mutation studies with formaldehyde, Rapoport (1947) obtained 2 to 6 per cent sex-linked lethal mutation rates after soaking 15-24 hours old eggs in 2 and 4 per cent solutions of this chemical substance for one hour. On the other hand, Auerbach (1952) reported a series of experiments in which 5-20 hours old chorionated and dechorionated eggs failed to mutate after 1 or 2 hour immersions in 2-5 per cent solutions of formaldehyde. Although those experiments failed to confirm Rapoport's results, another experiment in the same paper (Auerbach, 1952), which was submitted for publication after her 1953 paper was read, yielded a mutation rate of 7.4 per cent after 16-20 hours old eggs were treated through an agar block which was flooded for two hours with 5 per cent formaldehyde. Considering the mutagen to be effective for 24 hours, the ages which were subject to treatment in this case therefore ranged from 16-46 hours post oviposition. Now since the agar slab was repeatedly washed after the two hour period of treatment, either the residue of mutagen remaining after washing and after 14 hours of mutagenic decay was able to produce 7.4 per cent of lethal mutations in 10 hours by acting more powerfully than this on the fraction of larvae which were oldest, or some stage prior to 36 hours of development was capable of mutagenic response. That the latter is true can be seen from the data of table 1 where individuals treated beginning 0-12 hours after oviposition (and therefore subject to mutagen between 0 and 36 hours after oviposition) had a 7.7 per cent mutation rate. This mutation rate is statistically higher ( $P < .01$ ) than the rate in individuals 12-24 hours old at the time of treatment, and not different from the rates from individuals 24-36 hours old (9.2 per cent) or 36-48 hours old (7.6 per cent) when treated.

Since it is possible for females to hold eggs for some hours after fertilization before laying them, if individuals from such eggs were used in the present experiments they would have been older when treated than reckoned above. However, the inclusion in the 0-12 hours old group of 12 to 24 hours old individuals would have lowered the mutation rate of this group, while the presence of older flies in the 12-24 hours old group would have increased its mutation rate. Thus, the presence of individuals which are older than calculated would mean that the observed differences were smaller than the actual ones. To insure, as far as possible, that the number of retained eggs was minimal in this work, oviposition was encouraged by keeping males in the presence of the females, and fresh food medium was

supplied to parents every 12 hours. Although the number of retained eggs under such conditions in the last 4 transfers of a total of 16 successive ones would seem negligible, the procedure of taking 4 approximately equal samples of males emerging on successive days from each bottle meant that the first males to complete development could only comprise about one-fourth of the sample from each bottle. Finally, since the lethals were obtained from so high a proportion of the approximately 100 males tested in each of the four groups, as to make it highly unlikely that a considerable number of the induced mutations occurred in just this small minority of individuals of advanced ages, it is concluded that the ages of the groups treated did not vary appreciably from those given in the table, and the mutation rates obtained from them are sufficiently decisive.

In view of the numerous factors potentially capable of influencing the reaction of germ cells to mutagens, which have been discussed in detail by Auerbach (1953), it does not yet seem necessary to consider mutation rates for different stages in development as a direct reflection of the sensitivity of germ cells to the mutagenic agent. Moreover, it can be seen that the extension of formaldehyde mutability to a number of different stages in male sex cell development, not only has complicated any view of sensitive stages for germ cells in males but has removed the basis for the application of such a view to an explanation of the non-mutability of formaldehyde in females.

#### SUMMARY

The ability of formaldehyde to induce sex-linked recessive lethal mutations in germ cells of male *D. melanogaster* has been extended, from spermatozoa and the developing germ cells of individuals 36 hours of age and older, to an earlier stage in which treatment was started at 0-12 hours of age and could have lasted until 36 hours of development. The mutation rate of 7.7 per cent obtained for this stage was not significantly below that found for individuals 24-36 (9.2 per cent) or 36-48 (7.6 per cent) hours old at the time formaldehyde was administered, although the 4.2 per cent mutation rate for the 12-24 hours old individuals was significantly lower ( $P < .01$ ) than the rate of the three other stages when combined and of the rates for the stages just preceding or following when tested separately. The results are interpreted as demonstrating that the mutagen loses a large proportion of its potency within a period of twelve hours.

#### ACKNOWLEDGEMENT

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THE ROLES OF HEREDITY AND ENVIRONMENT  
IN ONTOGENETIC ADAPTATION

FREDERICK E. WARBURTON

3615 University Ave., Montreal, P.Q. Canada

The most fundamental law of genetics may be stated in the form: "Many morphological types may develop in a given environment; which of these types will develop is determined by heredity. Also, many morphological types may develop within a given genotype; which of these types will develop is determined by the environment." This mode of expression avoids the fallacy pointed out by Woodger (1952) who rigorously demonstrates that it is illogical to say that either heredity or environment alone determines the nature of the organism. Since both are equally necessary, neither can be more important, just as neither voltage nor resistance can be more important than the other in determining the size of an electric current.

The actions of heredity and environment are related in another manner of great importance, which may be stated in the rule: "If two organisms of similar genotype develop in different environments, the morphology of each will be better adapted to the environment in which it develops than to the other environment, in many more cases than we would expect from chance alone."

Morphological differentiation of this nature may be called ontogenetic adaptation; examples should be familiar to any biologist. The hypertrophy of muscles in response to exercise, of one kidney to compensate for surgical removal of the other, and of the thyroid to compensate for dietary lack of iodine are common clinical illustrations. The trabeculae of a bone during healing of a fracture arrange themselves in response to the prevailing forces acting on the bone. Bizzozero found that if the two ears of a young rabbit were maintained at different temperatures, the warmer ear grew conspicuously larger than the other, as though adapting itself to the more rapid dissipation of heat. These and many other examples are discussed by Wright (1950). Men and experimental animals transferred to high mountainous regions develop an increased haemoglobin concentration, compensating for the reduced atmospheric oxygen tension (Whitby and Britton, 1939). Individuals of the American oyster, *Crassostrea virginica*, grow long and narrow when exposed to a constant heavy fall of silt, thus keeping the lip of the shell above the steadily rising mud surface. The formation of calluses as a response to friction, the tanning of human skin, offering protection from ultra-violet radiation, and the growth of dense fur by tropical mammals exposed to northern winters (as by the baboons in the Riverdale Zoo, Toronto) are other familiar examples. The list could be immensely expanded.

Any theory used to explain the action of genes during development must, to be acceptable, describe how genes control developmental processes with

sufficient flexibility to allow the environment to exert its equally important effect, and must explain how the resulting morphology is so often appropriately describable as the "best possible" for its particular environment. The last requirement may appear to make a mechanistic hypothesis extremely difficult to formulate, but it actually acts as a guide toward a simple interpretation of developmental genetics which receives at least fragmentary support from published evidence and which is not contradicted by any facts with which the writer is acquainted.

Adaptability is, of course, selectively advantageous, and natural selection would have an important place in any discussion of the evolution of adaptability. To say this, however, is not to explain the mechanism of adaptation. Natural selection explains only how genes become established within a population; as Darwin well knew, it casts little light on the mechanism of heredity.

If we consider an organism to be divided into an arbitrarily large number of minute spatial regions, its morphology may be described in terms of the quantity of each of many chemical substances within each region. During development, these quantities change with time, but the rate of change of quantity of any substance within a given region is always the resultant of, (a) the additive rate, which is the sum of the rates of immigration of the substance into the region and of its formation from pre-existing substances within the region, and, (b) the subtractive rate, which is the sum of its rate of emigration from the region and of its consumption in the formation of other substances within the region. Thus, if "y" is the quantity of a given substance in a given region,  $dy/dt = \text{additive rate} - \text{subtractive rate}$ .

But  $dy/dt$  is frequently dependent on the value of "y." For example, haemorrhage or an unnecessary transfusion in man changes either the additive or the subtractive rate of haemoglobin formation until its concentration has returned to its normal value. Rose (1952) has shown that removal of part of the liver of a mouse results in accelerated liver growth, and that the addition of cells of certain types to the medium in which an embryo is developing inhibits the differentiation of similar cells in the embryo. Thompson (1948) has pointed out the relation of growth rate to size attained, and the inverse relationship of the rate of organ regeneration to the size of the stump. It is therefore descriptively correct to say that either the additive or the subtractive rate, or both, is a function of "y." I.e.,

$$dy/dt = f(y) - g(y) \quad (I),$$

where  $f(y)$  and  $g(y)$  are both rates of physiological processes and, as such, must be dependent on the physiological states of the organs in which they take place. But if these rates are dependent on the value of "y" the physiological states of the organs in which they occur must also be dependent on the value of "y." Thus, the general metabolic rate of the body is affected by its size, and the additive and subtractive rates of body size prove to be dependent, as different functions, on body size (Bertalanffy, 1951). Rose (1952) suggests that the liver produces a metabolite in quantities de-

pendent on its size which, he postulates, affects liver physiology in such a way as to retard its growth. We may hesitate to accept this assumption and merely agree with Bertalanffy and Pirozynski (1952), Thompson (1948) and many others that the physiological effect of an organ (presumably on itself as well as on the body as a whole) depends on its size. The rate of growth of a rabbit's ear seems to depend on temperature, which falls as the ear grows larger; the rate of deposition (or removal) of melanin by human skin cells apparently depends on the intensity of light reaching the deeper cells, which in turn is affected by the melanin concentration. We may speculate that the rate of haemoglobin destruction in the body rises as the oxygen tension of the blood rises in those organs in which erythrocyte destruction occurs. In each such case it is the physiological state of the organ concerned which controls the additive or subtractive rate and which is in turn affected by the value of "y."

The ratio of the additive to the subtractive rate changes throughout development until, when growth is complete, the two rates are equal and the organism has attained a morphological steady state. In the steady state, construction and destruction are constantly going on, but at the same rate. That organisms attain such dynamic steady states was shown by Schoenheimer (1942) using tracer isotopes, and hundreds of experiments have offered supporting evidence since; historically, the idea is very old. Since the additive and subtractive rates depend on the physiological states of the organs in which the processes occur, their equality in the steady state implies that these organs have attained a particular physiological state; and if other things are constant, this implies that "y" has reached a definite value.

But other things are not necessarily constant. The physiological state of an organ depends not only on the value of "y" but also on the values of certain environmental parameters. For example, the oxygen tension within blood-destroying organs of the human body depends on both the haemoglobin concentration of the blood and the partial pressure of the oxygen of the atmosphere; the temperature of a rabbit's ear depends on its area, but also on the ambient temperature; the intensity of irradiation of deep skin cells depends not only on the density of melanin in the superficial layers, but also on the intensity of light to which the superficial skin is exposed; the amount of tension acting at a given point in a bone depends not only on the arrangement of trabeculae within the bone, but on the posture and activity which the environment imposes on the animal.

Previously we have called the additive and subtractive rates, respectively,  $f(y)$  and  $g(y)$ , on the tacit assumption that "y" was the only variable affecting the physiology of the organs involved. If we now consider an environmental parameter of value "E," which also has a physiological effect, equation (I) must become  $dy/dt = F(E,y) - G(E,y)$ . During development, "y" will continue to change until the expression reaches such a value that  $F(E,y) = G(E,y)$ , when a steady state will be attained. If "E" varies from one case to another, the value of "y" in the steady state will also vary,

but since the physiological state depends on the value of the entire expression ( $E, y$ ), it will be the same in any steady state. In other words, the morphological steady state of the organisms will vary in such a way as to produce the same steady physiological state in all environments.

A numerical example (intended to correspond only very roughly with reality) may clarify this concept. Let "E" be the intensity of ultraviolet light reaching the superficial skin; let "y" be the intensity of pigmentation of the skin, in units so chosen that the intensity of light reaching the deep skin cells is  $E/y$ ; suppose also that  $F(E, y) = 2E/y - 10$ ; and  $G(E, y) = E/y$ . Then the steady state will be reached when  $F(E, y) = G(E, y)$ , i.e., when  $E/y = 10$ , that is, if the intensity of superficial illumination increases tenfold, the pigmentation of the skin will also increase tenfold before the steady state is attained; but, no matter what the intensity of surface illumination, the density of pigmentation will change in such a way that the illumination of the deep skin cells, in the steady state, will always have a value of 10.

Similar illustrative use could be made of each of our examples. If atmospheric oxygen becomes scarce, haemoglobin concentration will rise until the oxygen tension in blood-destroying organs regains its former value. If the stresses to which a bone is subject change, tissue will be absorbed or deposited until trabeculae again lie along lines of stress and not along lines of shear. If the ambient temperature rises, the rabbit's ear grows until it is radiating heat rapidly enough to restore its original temperature.

It has long been suspected that genes may operate by affecting the rates of processes within the organism (Wright, 1941) perhaps by determining the nature of the enzymes involved. If the former hypothesis is correct, whether the latter is or not, genes determine the reaction constants of the various processes taking place in the organism, i.e., the nature of the functions "F" and "G" used above. That is, they determine the rates at which processes will occur in a given set of physical and chemical (i.e., physiological) conditions. They thus cannot determine the morphological state at which additive and subtractive processes will have equal rates, but only the physiological conditions in which a steady state will occur.

If, then, genes affect development by controlling the rates of processes, it may be said that the final steady physiological state of an organism is determined by its heredity; its final morphological state will then be that particular form which will produce the genetically determined physiological state in the particular environment in which development occurs: the organism will therefore automatically adapt itself to its environment.

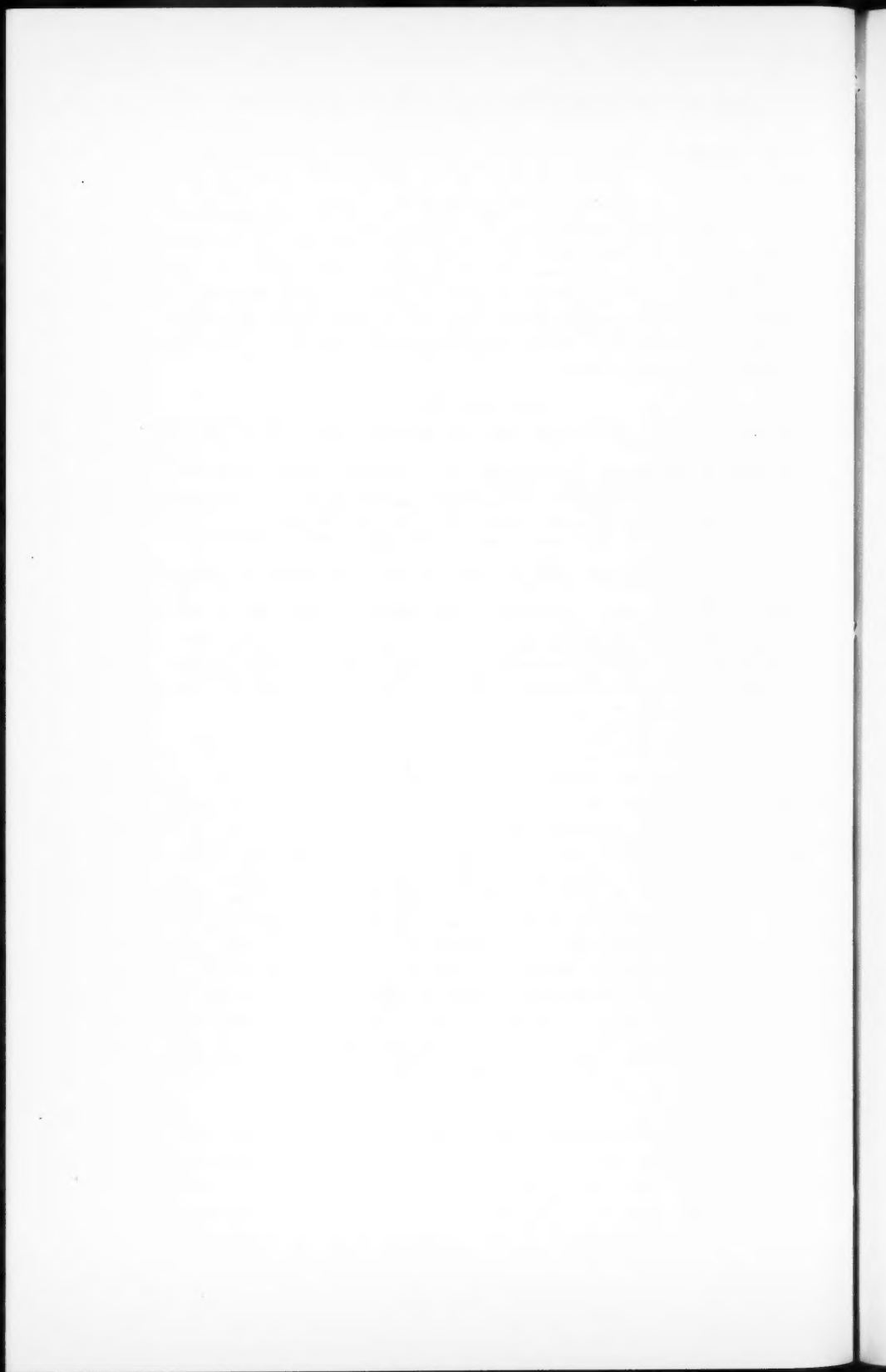
#### SUMMARY

The development of organisms involves simultaneous, opposed additive and subtractive processes. When the rates of such paired processes are equal, the organism has reached a dynamic steady state which is its final morphology. But such processes are physiological processes, and can be affected only by the physiological state of the organs in which they occur.

If the environment exerts an effect on the physiological states of such organs, the steady (morphological) state will be shifted until it and its interactions with the environment serve to bring about the particular physiological state required for the equality of the additive and subtractive processes. If genes operate by determining reaction constants, for example, by determining the nature of the enzymes involved in developmental processes, they can determine only the physiological state in which a steady state will be reached, and the final morphological state will be that required to produce the genetically determined physiological state in the particular environment in which development occurs.

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COMPARATIVE GENETICS OF *DROSOPHILA*  
*TRIPUNCTATA* LOEW

JACK BENNETT

Department of Zoology, Washington University, St. Louis, Missouri\*

The comparative genetics of *Drosophila* holds promise of shedding considerable light on the mechanisms of evolution within the group. Over the past forty years information about genetic homology has been accumulating for the many species of the genus. Sturtevant and Novitski (1941) brought together most of the material then available, and were able to show that in many cases enough data were at hand to establish homologies between the several species compared.

The author considers *Drosophila tripunctata* Loew to be a desirable object of study for several reasons. The range of the species overlaps the ranges of *D. robusta* and the *D. americana-texana* species complex. Both of the latter have been the subjects of considerable investigation (Stalker and Carson, 1947, 1948, 1949; Carson and Stalker, 1946, 1947, 1949; Patterson and Stone, 1952) and have demonstrated two very different patterns of population structure and evolutionary behavior (Carson, 1952). As a fungus breeding species, *D. tripunctata* represents an ecological group which has been subject to little genetic analysis. It is the sole representative in the United States of the ubiquitous South American *medio-* (*tripunctata*) group, which has been the object of taxonomic and ecological investigation, e.g., Dobzhansky and Pavan, 1950. Thus of itself and for comparison with other species, *D. tripunctata* offers a fertile field of research.

The raw materials of comparison in this study are described mutant genes and a knowledge of their locations as to linkage group. Since in many cases there are several different genes known with identical, or nearly identical, phenotypic expression, comparison of single genes may be in many cases misleading or impractical. In the case of a few distinctive genes, with no known mimics, in a well studied species, a definite and fairly reliable decision can be made as to homology.

*Drosophila melanogaster* has more known mutant loci than any other species, and thus offers a unique basis for the comparison of the many species in the genus. A comprehensive monograph of the known loci of *D. melanogaster* has been published by Bridges and Brehme (1944). This monograph has served as the prime reference for comparison of genes in this study.

Spencer (1949) may be consulted for a discussion of the methods and criteria used in establishing homology, and for a discussion of homology between chromosome arms. Muller (1940) suggested the use of the chromosomes of *D. melanogaster* as a basic standard, and used the word "element" to describe the individual chromosome arm. Thus the X-chromosome

\*Present address: Department of Zoological Sciences, The University of Oklahoma, Norman, Oklahoma.

of *melanogaster* is designated element A, the left arm of the second chromosome (IIL) as B, the right arm (IIR) as C, the left arm of the third chromosome (IIIL) as D, the right arm (IIIR) as E, and the small fourth chromosome (IV) as element F. This system has been used by Sturtevant and Novitski (1941) and others, and will be used here.

Metz (1916), Sturtevant (1921) and Wharton (1943), have published figures of the metaphase configuration of *D. tripunctata*. Observations of aceto-carmine squash preparations of *tripunctata* ovaries, (kindly prepared by Mr. W. C. Blight), confirm the published figures as to chromosome number. Gonial mitoses show two pairs of long chromosomes, three pairs of medium length chromosomes and a pair of dot chromosomes. All of the major chromosomes appear to be of the rod type, with terminal or subterminal centromere. The X-Y pair has not been identified.

Four linkage groups are known in *D. tripunctata*, (designated II, III, IV, and V). Dr. H. D. Stalker (unpublished) has identified three of these autosomal linkage groups and the author a fourth (see table 1). From the chromosome complement of the species, two additional groups, one showing sex-linkage, are expected, but as yet no mutant genes have been found for them.

TABLE 1  
THREE AUTOSOMAL LINKAGE GROUPS OF *Drosophila tripunctata* AND THEIR  
MUTANT LOCI, AS IDENTIFIED BY H. D. STALKER (UNPUBLISHED)

Autosomal linkage group	Mutant loci composing the linkage group
II	<i>rough</i> , <i>shortvein</i> , <i>crossveinless</i> , <i>erect</i> , <i>peach</i> , <i>brown</i> , <i>cardinal</i> , <i>broad</i>
III	<i>scarlet</i> , <i>ruby</i> , <i>approximated</i>
IV	<i>plum</i>

The usefulness of the eye color mutants is limited. There are often a variety of shades of color produced by the alleles at any one locus, and the wild type colors themselves differ between species, making absolute color comparisons of little value. Mutant genes which produce structural changes are more useful, but the decision that one is an allele or homolog of a similar mutant in another species is at best a very good guess (unless hybridization is possible). Eye color comparisons are likely to have little significance unless their linkage relationships with structural mutants are well known. They have been included in this analysis, not because they are reliable in themselves, but because they lend some slight support to the other evidence.

Linkage group II contains six loci for comparison, as follows:

1. *rough eye* (*ro*). Eye color unaffected, facets are normal, hairs are irregular. This is a parallel to *pebbled* or possibly *ommatidia* of *D. melanogaster*, both on element A.
2. *crossveinless* (*cv*). Both anterior and posterior crossveins always missing, wings occasionally show slight waviness. This is a parallel of *crossveinless* in element A.

3. *brown eye (bw)*. An eye color intermediate in shade, between *brown* and *sepia* as pictured in plate 1, Sturtevant and Beadle (1939), and gradually darkening with age, always easily classifiable, adult testes colorless. This could be a parallel to many *melanogaster* eye mutants, but is, perhaps, closest to *ruby* or *garnet*, both on element A.
4. *peach eye (pc)*. Phenotypically like *garnet*<sup>2</sup> and *brown* as pictured by Sturtevant and Beadle (1939). Adult testes colorless, no other known effects in larvae or adults. Darkens with age. This seems similar to *Henna-recessive* of element D, or to sepiaoid of element E. (This mutant eye color is phenotypically very close to *plum* of *D. tripunctata*.)
5. *shortvein (so)*. A wing mutant, varies in expression from a short gap near distal end of L2, to large missing distal portions of L2, L4, L5, and (rarely) L3. Usually L3 is not affected, but if affected, only slightly so. No other known effects in larvae or adults. Similar to *veinlet* of element D, or *vein-longitudinally-shortened* which is either on D or E.
6. *erect bristles (er)*. Posterior scutellar bristles point vertically or anteriorly (in side view) and cross sharply. Wings tend to be curled or wavy, not highly viable and not always easy to classify. Larvae unaffected. This is a parallel of *curled* on element E, or perhaps *Erect* also on element E.

Linkage group III has two usable mutant genes as follows:

1. *scarlet eye (st)*. An eye color as bright or brighter than *vermillion* as pictured by Sturtevant and Beadle (1939). Does not change with age, ocelli slightly lighter than wild type. Adult testes paler than wild type but not colorless. No other known morphological effects in larvae or adults. Adults show a 25% to 50% increase in rate of Oxygen consumption as compared to wild type. This is a parallel to *vermillion* of element A.
2. *approximated (app)*. A wing mutant, the crossveins moved closer together, the posterior crossvein shifted the most. The sum of the lengths of the two crossveins is equal to or greater than the distance between them. Adult body, tarsi, scutellar bristles, and the larvae appear normal. This is a parallel to *dachsous*<sup>2</sup> of element B.

Linkage groups IV and V have only one known locus each. In group IV *plum* eye color by itself is completely unreliable for establishing homology. In group V:

*eyeless (ey)*. Reduces the size of the eyes irregularly, reduction all around the periphery, with eye occasionally broken into two or more sections by one or more horizontal breaks. Occasionally single facets on ends of stalks, or complete absence of eye with extra bristles and (rarely) an antenna-like appendage in the ocular area. Ocelli are wild type. Bilaterally eyeless flies have never been known to reproduce. Requires selection for small eyes to maintain stock, but even moderately affected individuals are suitable for outcrosses to other stocks. No other known effects on larvae or adults. This is a good parallel of *eyeless* on element F.

Table 2 summarizes the linkage groups of *D. tripunctata*, together with suggested homologies by element. It is apparent, upon inspection of the table, that no final statement should be made regarding homology between the linkage groups of *D. tripunctata* and those of other *Drosophila* species. However, a tentative interpretation of the material would indicate that linkage group II in *D. tripunctata* is homologous to portions of elements A and E, and that group III may be homologous to the balance of element A and element B. The close correspondence of the distinctive mutant *eyeless* to its namesake on element F, may be taken as a strong indication that group V is homologous to element F.

TABLE 2  
CHROMOSOME HOMOLOGIES OF *Drosophila tripunctata* AS  
SUGGESTED BY CERTAIN MUTANT GENES

Linkage group of <i>D. tripunctata</i>	Mutant gene of <i>D. tripunctata</i>	Suggested homologous element of <i>D. melanogaster</i>
II	<i>rough</i>	A
II	<i>crossveinless</i>	A
II	<i>brown</i>	A
II	<i>erect</i>	E
II	<i>shortvein</i>	E or D
II	<i>peach</i>	E or D
III	<i>approximated</i>	B
III	<i>scarlet</i>	A
V	<i>eyeless</i>	F

Spencer (1949), and Sturtevant and Novitski (1941) have shown that there is considerable evidence that in the evolution of many species of *Drosophila* the chromosome elements have remained largely intact. That the elements have in some cases broken up and been redistributed has been shown by Wharton, 1943; Spassky, Zimmering and Dobzhansky, 1950; and Spassky and Dobzhansky, 1950. It seems likely that as more material accumulates, cases of both kinds will continue to appear. The existence of a strong deterrent influence on the breaking up of chromosomes in *Drosophila* evolution is demonstrated by the fact that in many species the elements have remained largely intact, even though there are so many ways that change may occur that we might have expected to find no interspecific homology.

The evidence presented here could be taken to indicate, but does not prove, that the evolution of *D. tripunctata* has involved an interchange of portions of the "original" (as represented by *D. melanogaster*) chromosome elements, thus adding to the list of those cases where a "breaking up" of the elements has apparently occurred.

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#### SUMMARY

1. A discussion is presented of the probable homology of several of the mutant genes in *D. tripunctata* with those of *D. melanogaster*.

2. Possible homology is suggested between: linkage group II of *D. tripunctata* and portions of elements A and E of *D. melanogaster*; linkage group III and portions of elements A and B; and finally between linkage group V of *D. tripunctata* and element F of *D. melanogaster*.

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## PUBLICATIONS RECEIVED

THE AMERICAN NATURALIST is glad to acknowledge here the receipt of books on biological and natural history subjects which are likely to be of interest to our readers. No undertaking to publish reviews is implied in this acknowledgment. Books for notice may be sent to:

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Brown, R., and J. F. Danielli, Editors, 1953. *Symposia of the Society for Experimental Biology*, No. VII: *Evolution*. 448 p., 4 plates, 50 figures. \$7.80. Academic Press, Inc., New York.

Twenty-two papers on evolution in all organisms, from bacteria to the higher plants and man, with a foreword by J. B. S. Haldane and a postscript by J. F. Danielli. The articles cover a variety of topics, such as the Origin of Life (J. W. S. Pringle), Biochemistry and Evolution (E. Baldwin), Stochastic Processes and the Growth of Bacterial Colonies (D. G. Kendall), The Genetic Structure of Populations (K. Mather), Race Formation and Reproductive Method in Flowering Plants (H. G. Baker), Evolutionary Trends in Equatorial Climate (R. E. Holttum), Epigenetics and Evolution (C. H. Waddington), Genetics of Specific and Subspecific Differences in European Newts (H. Spurway), Polymorphism and Population Studies (P. M. Sheppard), Locomotory Habits and the Evolution of the Larger Arthropodan Groups (S. M. Manton), and Social Behavior and Primate Evolution (M. R. A. Chance and A. P. Mead).

Some of these articles, such as those of Baker, Spurway, and Sheppard, present valuable new data; other, like those of Baldwin and Manton, are original and penetrating analyses of more or less well-known facts; while a third type, represented by the contributions of Pringle, Mather, and Waddington, present theoretical concepts of wide general interest.

The articles are all modern and forward looking. They are further evidence of the great progress being made in experimental evolution at the present time. Since most of the outstanding British workers in this field are represented among the contributors to the volume, the biologist can obtain from it a very good impression of the current trend of thought among British evolutionists.

The new data are particularly valuable to American biologists interested in making generalizations about evolution because they concern for the

most part organisms which are relatively little studied in the United States. Instead of the well-known examples of *Drosophila*, *Peromyscus*, *Rana*, maize, *Gossypium*, and *Potentilla*, we learn about various Lepidoptera, *Clethrionomys* (a vole), *Triturus*, *Armeria*, *Primula* and the ferns. The fact that generalizations about population and other data in these organisms are essentially similar to those made by American evolutionists about the organisms familiar to us is further evidence that we are finally beginning to understand many of the basic processes of evolution. Most of the authors indulge freely in theoretical speculations, but these are in general well supported by the facts considered, and are particularly stimulating to the reader who is looking for ideas. The volume is a "must" for all biologists actively engaged in evolutionary studies.

G. LEDYARD STEBBINS

Davies, R., and E. F. Gale, Editors, 1953. *Adaptation in micro-organisms*. Third symposium of the Society for General Microbiology held at the Royal Institution, London, April, 1953. 339 p., ill. \$6.00. Cambridge University Press, New York.

The first three papers in this symposium are on the broad introductory topic of the evolutionary interpretation of adaptations in micro-organisms and are contributions of R. Y. Stanier, A. C. R. Dean and Sir Cyrol Hinshelwood, and A. W. Ravin. The next four papers deal with the problem of enzyme adaptation, emphasizing the value of this phenomenon in gaining an insight into the nature of enzymes and their precursors. P. Slonimski, S. Spiegelman and H. O. Halvorson, M. Cohn and J. Monod, M. R. Pollock and R. Knox are the contributors to this section. The third group concerns various problems involved in the development of drug resistance in micro-organisms. There is a general paper on the subject by E. P. Abraham, while M. Barber and D. A. Mitchison in separate papers deal with the development of drug resistance in specific virulent organisms. A very interesting paper by L. F. Hewitt on the influence of bacteriophage on bacterial variation also belongs to this group. The last three papers, concerned with a general survey of adaptive responses in different groups of micro-organisms, are by G. H. Beale on *Paramecium*, L. F. L. Clegg and S. E. Jacobs on Thermopiles, and W. Brown and R. K. S. Wood on Fungi. The quality of the papers and the ensuing discussions which are included is excellent, and the material is such that biologists, biochemists, and medical men alike will find this volume of value.

S. GARTLER

